A Review of the Extinct Wolverine, *Plesiogulo* (Carnivora: Mustelidae), from North America

JESSICA A. HARRISON

SMITHSONIAN CONTRIBUTIONS TO PALEOBIOLOGY • NUMBER 46

SERIES PUBLICATIONS OF THE SMITHSONIAN INSTITUTION

Emphasis upon publication as a means of "diffusing knowledge" was expressed by the first Secretary of the Smithsonian. In his formal plan for the Institution, Joseph Henry outlined a program that included the following statement: "It is proposed to publish a series of reports, giving an account of the new discoveries in science, and of the changes made from year to year in all branches of knowledge." This theme of basic research has been adhered to through the years by thousands of titles issued in series publications under the Smithsonian imprint, commencing with *Smithsonian Contributions to Knowledge* in 1848 and continuing with the following active series:

Smithsonian Contributions to Anthropology
Smithsonian Contributions to Astrophysics
Smithsonian Contributions to Botany
Smithsonian Contributions to the Earth Sciences
Smithsonian Contributions to the Marine Sciences
Smithsonian Contributions to Paleobiology
Smithsonian Contributions to Zoology
Smithsonian Studies in Air and Space
Smithsonian Studies in History and Technology

In these series, the Institution publishes small papers and full-scale monographs that report the research and collections of its various museums and bureaux or of professional colleagues in the world of science and scholarship. The publications are distributed by mailing lists to libraries, universities, and similar institutions throughout the world.

Papers or monographs submitted for series publication are received by the Smithsonian Institution Press, subject to its own review for format and style, only through departments of the various Smithsonian museums or bureaux, where the manuscripts are given substantive review. Press requirements for manuscript and art preparation are outlined on the inside back cover.

S. Dillon Ripley
Secretary
Smithsonian Institution

SMITHSONIAN CONTRIBUTIONS TO PALEOBIOLOGY • NUMBER 46

A Review of the Extinct Wolverine, *Plesiogulo* (Carnivora: Mustelidae), from North America

Jessica A. Harrison

SMITHSONIAN INSTITUTION PRESS
City of Washington
1981

ABSTRACT

Harrison, Jessica A. A Review of the Extinct Wolverine, *Plesiogulo* (Carnivora: Mustelidae), from North America. *Smithsonian Contributions to Paleobiology*, number 46, 27 pages, 16 figures, 1981.—There are two fossil species of *Plesiogulo* in North America: *Plesiogulo marshalli*, to which most of the fossil material is herein referred, and *P. lindsayi*, new species. Both species are restricted to the late Hemphillian. A formal diagnosis is offered for *P. marshalli*. Remains of *Plesiogulo* are relatively rare, possibly due to low densities in extinct populations. The only known juvenile specimens of *Plesiogulo* are from the Edson Local Fauna, where three juveniles together with a single mature individual probably represent a female with a litter of cubs. *Plesiogulo* migrated to the New World some time between 7.0 and 6.5 million years ago. This taxon, generally interpreted as an inhabitant of forest or woodland, was probably equally well adapted to the open plains.

OFFICIAL PUBLICATION DATE is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, *Smithsonian Year*. SERIES COVER DESIGN: The trilobite *Phacops rana* Green.

Library of Congress Cataloging in Publication Data
Harrison, Jessica A.
A review of the extinct wolverine, Plesiogulo (Carnivora, Mustelidae)
(Smithsonian contributions to paleobiology ; no. 46)
Bibliography: p.
Supt. of Docs. no. : SI 1.30:46
1. Plesiogulo. 2. Paleontology—Pliocene. 3. Paleontology—North America. I. Title. II. Series.
QE701.S56 no. 46 [QE882.C15] 560s [569'.74] 81-607075 AACR2

Contents

A Review of the Extinct Wolverine, *Plesiogulo* (Carnivora: Mustelidae), from North America

Jessica A. Harrison

Introduction

Plesiogulo, an extinct relative of the living wolverine *Gulo*, is known from 14 Hemphillian localities in North America. Remains, however, are seldom abundant, and at only a handful of localities are more than one or two individuals represented. Although complete skulls and mandibles have been recovered from Old World localities, most notably those in the Paote area of the People's Republic of China, the North American material consists, for the most part, of partial dentitions and isolated teeth.

Although *Plesiogulo* has been recorded in the literature from seven localities, several additional localities and the bulk of the fossil material remained undescribed. In 1928, H. T. Martin designated a nearly complete right ramus from the Edson Local Fauna as the type of *Brachypsalis marshalli* and referred a C^1 and a maxillary fragment bearing P^4-M^1 Shortly thereafter, Hibbard (1934) transferred this material to *Plesiogulo* in a faunal list. Matthew and Stirton (1930), Reed and Longnecker (1932), and Sellards, Adkins, and Plummer (1932) produced lists of the mammals from the type Hemphillian Coffee Ranch Local Fauna of Texas, but none contained *Plesiogulo*. Hesse (1936:67) indicated the presence of *Plesiogulo* at Coffee Ranch, and Savage (1941:705) listed ?*Plesiogulo* from Optima (=Guymon), Oklahoma, but in neither paper was the nature of the fossil material discussed. Shotwell (1955:332) also included *Plesiogulo* in a faunal list of Coffee Ranch, and he (1956:733) identified as *Plesiogulo* sp. an associated P^4-M^1 and an isolated M_1 from McKay Reservoir in Orgeon. Wilson (1968:111) erroneously referred to *Plesiogulo* an isolated M^1 from the WaKeeney Local Fauna of Kansas. In 1969:11 Dalquest referred to *P. marshalli* an isolated M^1 and a partial M_1 from Coffee Ranch. Schultz (1977:75) confirmed the presence of *Plesiogulo* in a list of the Optima Local Fauna. MacFadden (1977:789) noted a palate of *Plesiogulo* sp. from San Juan Quarry, New Mexico. McFadden, Johnson, and Opdyke (1979:357) referred the material from the Wikieup Local Fauna, Arizona, to *P. marshalli*; this material constitutes the hypodigm of *P. lindsayi*, new species, described herein. Baskin (1979, fig. 2) illustrated an isolated M^1 of *Plesiogulo* from the White Cone Local Fauna of Arizona, and Bennett (1979:5) referred an isolated P^4 from Lost Quarry, Kansas, to *P. marshalli.*

GENERIC RELATIONSHIPS.—The general resemblance of *Gulo* and *Plesiogulo* has been noted by many workers (Miller, 1912:433; Zdansky, 1924:

Jessica A. Harrison, Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

38; Webb, 1969:65). Viret (1939:15) and Kurtén (1970:20) maintain that *Plesiogulo*, in particular *P. monspessulanus*, was ancestral to *Gulo*. However, I agree with Zdansky (1924:44) and Webb (1969: 65) that such a line of descent would require an inordinate number of evolutionary reversals.

As early as 1912, Miller (1912:432) advocated a separate subfamily, the Guloninae, for *Gulo*. This classification was followed by Pocock (1920: 187), who also agreed with Gill (1872:66), that *Mellivora* should be placed within its own subfamily, the Mellivorinae. Webb (1969:68) supported the removal of *Gulo* from the Mustelinae, but placed it instead in the Mellivorinae, where, together with *Plesiogulo*, *Hadrictis*, and *Ischyrictis*, it constituted the Gulonini. The subsequent discovery of new fossil mustelids exhibiting gulonine/ mellivorine affinities (Bryant, 1968:2; Bjork, 1970:19), in addition to new material of existing taxa (Hendey, 1978:330), further complicates the phylogeny of this interesting group of carnivores.

PALEOECOLOGY.—The diet of *Gulo* consists chiefly of meat, augmented in the summer months by berries, eggs, and wasp larvae (Myhre and Myrberget, 1975; Krott, 1960). A large percentage of the meat is carrion. Although *Gulo* possesses both the strength and ferocity requisite for the taking of large prey, smaller animals such as rodents, birds, fish, and frogs are also common dietary items (Grinnell, Dixson, and Linsdale, 1937:268; Jackson, 1961:362). Morphological similarities in the dentition of *Plesiogulo* suggest that this taxon was also such a broad-based, opportunistic feeder. The size and stoutness of the premolar series argues that *Plesiogulo* could have masticated bone more efficiently than *Gulo*, but not, perhaps, with the virtuousity of hyaenids and borophagines.

Plesiogulo has traditionally been treated as an indicator of forest or woodland paleohabitat (Shotwell, 1958). This interpretation of *Plesiogulo* is based in part on the common misconception of *Gulo* as an animal largely restricted to boreal forest. However, *Gulo*, far from being an obligate forest-dweller, is very abundant in open tundra (Hall and Kelson, 1959; Krott, 1960; Nowak, 1973; and D. Wilson, pers. comm., 1979).

Plantigrady is not a common foot morphology for medium to large, eurytopic mammals; hence, in the minds of many researchers, flat feet have rendered *Plesiogulo* unfit for duty in treeless regions. While *Gulo* superficially appears to be plantigrade, and indeed leaves a rather flat track (Jackson, 1961), it is really digitigrade (Seton, 1929). Both *Plesiogulo* and *Gulo* are actually less "flat-footed" than either *Ursus* or *Thalarctos*, genera that frequent treeless habitats. Moreover, all three extant genera are noteworthy wanderers, *Gulo* traveling up to 40 miles (64 km) in a day.

Most of the fossil localities at which *Plesiogulo* occurs have not produced a sample of significant size, often no more than one individual. Only four localities have produced samples containing four or more individuals (Table 1); these are Optima, Coffee Ranch, Edson, and Wikieup. These faunas include many hypsodont grazers. Coffee Ranch, Edson, and especially, Optima contain large numbers of *Dinohippus interpolatus*. *Teleoceras*, although hardly a cursorial rhino, is extremely hypsodont. It occurs in great abundance at Optima, but is almost absent at Coffee Ranch and Edson. *Aphelops* is more cursorial than *Teleoceras*, but much more brachydont and is well represented at Coffee Ranch and Edson, but absent at Optima. *Texoceras*, a hypsodont, cursorial antilocaprid, is present in the hundreds at Optima, but less than half a dozen individuals are known from Edson or Coffee Ranch. Even after allowance is made for the much greater amount of fossil material recovered from Optima as opposed to Coffee Ranch or Edson, the difference in relative abundance of the aforementioned taxa is striking.

Savage's (1941:705) description of Optima during the Hemphillian as "an open plain or plains country with most of the forested areas confined to the river bottoms and stream valleys" is applicable as well to Coffee Ranch and Edson. A slightly greater representation of brachydont elements in the latter two faunas argues for slightly more woodland in their respective paleoenvironments. None of these localities, however, could be

interpreted as having been well forested, and, indeed, *Plesiogulo* is most abundant at Optima, the least forested locality.

In conclusion, it may be seen that the habitat, foot morphology, and behavior of *Gulo* do not support the restriction of *Plesiogulo* to a woodland habitat. The fossil record indicates that *Plesiogulo* was most abundant at localities interpreted as open plains with very limited woodlands. It seems probable that *Plesiogulo* was equally at home on the open plains or in the narrow belts of riparian woodland.

GEOGRAPHIC DISTRIBUTION.—*Plesiogulo* has been recovered from 14 North American localities (Figure 1). The majority of these are in the Southwest and southern Great Plains with outliers in Oregon, California, and Florida. Detailed knowledge of the geographic distribution in North America, as well as the morphology of *Plesiogulo*, is hampered by the rarity of this taxon. Only 5 localities out of 14 contain more than a minimum of one individual. Five localities contain only one specimen. The minimum number of individuals for each locality is listed in Table 1 together with the most abundant element upon which each respective calculation was based.

TABLE 1.—Population densities of *Plesiogulo* at 14 North American localities (elements used to calculate minimum number of individuals in Column 2 are listed in column 3; R. = right, L. = left)

Locality	*Minimum no. of individuals*	*Element*
Optima (Guymon)	6	R. P_4, R. M_1
Wikieup	4	R. M_1
Coffee Ranch	4	L. M^1
Edson	4	R. ramus
Ordnance (Westend Blowout)	2	maxilla
McKay Reservoir	1	R. P^4, R. M^1, R. M_1
Old Cabin Quarry	1	palate
Redington Quarry	1	R. C_1
San Juan Quarry	1	R. P^4-M^1
Pinole Tuff	1	L. P_4
Modesto Reservoir (Turlock Lake)	1	L. ramus
Bone Valley	1	L. M^1
White Cone	1	R. M^1
Lost Quarry	1	R. P^4

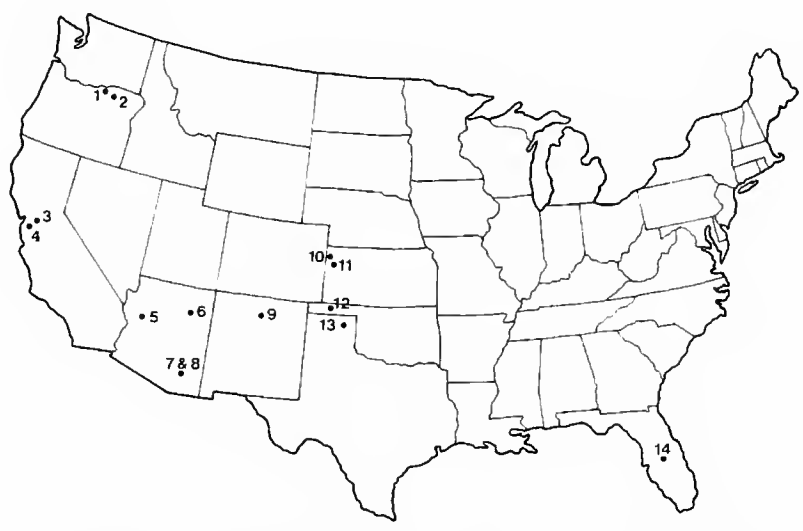

FIGURE 1.—Distribution of fossil localities known to contain *Plesiogulo* (1 = Ordnance (Westend Blowout), Oregon, 2 = McKay Reservoir, Oregon, 3 = Modesto Reservoir (Turlock Lake), California, 4 = Pinole Tuff, California, 5 = Wikieup, Arizona, 6 = White Cone, Arizona, 7 = Old Cabin Quarry, Arizona, 8 = Redington Quarry, Arizona, 9 = San Juan Quarry, New Mexico, 10 = Edson Quarry, Kansas, 11 = Lost Quarry, Kansas, 12 = Optima (Guymon), Oklahoma, 13 = Coffee Ranch, Texas, 14 = Bone Valley, Florida).

The paucity of fossil material may be due to low population density which may, in turn, be a function of extremely large individual territories. Large territories are characteristic of *Gulo*, the closest living relative of *Plesiogulo*. More important, morphological similarities between these two genera suggest that they were functionally similar. The stout premolars, shearing carnassials, and broad molars together with the low, cylindrical condyloid process, deep masseteric fossa, and wide zygomatic arch suggest that both genera were capable of ingesting an impressive array of dietary items, ranging from berries to bones. The postcrania indicate that both genera were unusually large in body and long-limbed for mustelids. Such functional similarity lends credence to ecological comparisons of *Plesiogulo* and *Gulo*.

Walker (1964:1204) states that a single male wolverine may share a territory of some 300,000 hectares (1158 sq mi) with two or three females. This would result in an average of one adult individual per 75,000 to 100,000 hectares (about 290–385 sq mi). Krott (1959) suggests even larger

territories for *Gulo*: up to 770 sq mi (about 200,000 hectares) for males and 150 to 190 sq mi (about 39,000 to 50,000 hectares) for females. Vast individual territories seem a reasonable explanation for the geographically widespread but poorly represented species of *Plesiogulo* in North America. However, the related Asian species, *P. crassa* (Teilhard de Chardin, 1945) appears to have attained much higher population densities. In excess of 30 skulls and 20 mandibles have been collected from the Paote localities of Shansi Province, People's Republic of China. They are housed in the Paleontological Institute at Uppsala, Sweden, and the American Museum of Natural History, New York.

Temporal Distribution.—Only 6 of the 14 faunas containing *Plesiogulo* are associated with radiometric dates. Three dates have been published for the ash overlying the Coffee Ranch Local Fauna. Boellstorff (1976:64) obtained a fission-track date on glass of 5.3 ± 0.4 m.y. Izett (1975:202) obtained both a younger date, also on glass, of 4.7 ± 0.8 m.y. and an older date, on zircon, of 6.6 ± 0.8 m.y. San Juan Quarry occurs 5 meters above the base of the upper tuffaceous zone of the Chamita Formation. MacFadden and Manley (1976) fission-track (zircon) dated an ash overyling the quarry, 5 meters below the top of the upper tuffaceous zone, at 5.6 ± 0.9 m.y. MacFadden, Johnson, and Opdyke (1979:360) also fission-track (zircon) dated the Big Sandy Formation containing the Wikieup Local Fauna at 5.5 ± 0.2 m.y. The White Cone Local Fauna is from the upper member of the Bidahochi Formation, and a basalt from the middle member has been K-Ar dated at 6.60 ± 1.6 m.y. (Scarborough, Damon, and Shafiquallah, 1974:472). Volcanic tuffs in the Quiburis Formation, which contains Redington Quarry and Old Cabin Quarry, have been K-Ar dated from 5.21 to 6.25 m.y. (Jacobs, 1977:505).

Wood et al. (1941:12) designated *Plesiogulo* as an index fossil of the Hemphillian Land Mammal Age, which was "based on the Hemphill Member of the Ogallala." The Hemphill "member," although not a distinct lithologic unit (Schultz, 1977:70), contains two faunas: the Higgins Local Fauna from the early Hemphillian and the Coffee Ranch Local Fauna from the late Hemphillian. Of these two, *Plesiogulo* occurs only in the younger Coffee Ranch Local Fauna, and moreover, has been found elsewhere only in faunas similar to that of Coffee Ranch. The faunas from Edson, Optima, McKay, Ordnance, Lost Quarry, Modesto Reservoir, Wikieup, Redington Quarry, and Old Cabin Quarry are all late Hemphillian in age, while those from San Juan Quarry and Upper Bone Valley are latest Hemphillian. Slightly older than Coffee Ranch and its correlatives, but still late Hemphillian in age, is the White Cone Local Fauna. The assessment of these faunas as late Hemphillian is corroborated by the presence of other immigrant genera, among them *Agriotherium* and *Machairodus*.

Plesiogulo is known from Old World faunas of Turolian (late Miocene) age. It is probable that sometime between 7.0 and 6.5 million years ago that this species migrated to the New World and rapidly extended its range across Canada and the United States. Glacial activity during the Pleistocene subsequently destroyed much of the more northerly late Miocene deposits; thus, remains of *Plesiogulo* are restricted largely to the southern half of the United States. The first appearance of *Plesiogulo* has come to be one of the criteria determining the late Hemphillian (R. H. Tedford, pers. comm., 1979).

Abbreviations.—The following abbreviations are used in this study:

AMNH	Department of Vertebrate Paleontology, American Museum of Natural History, New York, New York
F:AM	Frick Collection, American Museum of Natural History, New York, New York
KUVP	University of Kansas Museum of Natural History, Lawrence, Kansas
LACM	Los Angeles County Museum of Natural History, Los Angeles, California
MU	Midwestern University, Wichita Falls, Texas
TMM	Texas Memorial Museum, University of Texas, Austin, Texas
UCMP	University of California Museum of Paleontology, Berkeley, California

UF	Florida State Museum, University of Florida, Gainesville, Florida
UMMP	University of Michigan Museum of Paleontology, Ann Arbor, Michigan
UOMNH	University of Oregon Museum of Natural History, Eugene, Oregon
USNM	Former United States National Museum, collections now in National Museum of Natural History, Smithsonian Institution, Washington, D.C.

MEASUREMENTS.—Width of P^4 was measured across the protocone. Two anteroposterior dimensions of M^1 were measured: the lingual length refers to the maximum anteroposterior distance across the expanded inner lobe, and the median length refers to the minimum anteroposterior distance across the constriction at midcrown. Standard deviation was calculated only for samples of four or more.

ACKNOWLEDGMENTS.—I would like to thank Earl E. Manning and Henry Galiano, American Museum of Natural History, for their helpful comments and creative criticism. The following people did much to facilitate the loan of fossil specimens or comparative material: Walter W. Dalquest, Midwestern University; Eric Gustavsen, University of Oregon Museum of Natural History; Everett H. Lindsay, University of Arizona Laboratory of Paleontology; S. David Webb, Florida State Museum; Richard H. Tedford, American Museum of Natural History; J. Howard Hutchison, University of California Museum of Paleontology; and James E. Martin, South Dakota School of Mines and Technology. Additional material was borrowed from the University of Kansas Museum of Natural History and the Texas Memorial Museum. John Lance, National Science Foundation, and Hugh Wagner, University of California Riverside, provided elusive bits of information concerning particular specimens and localities. Donald E. Wilson, U. S. Department of Fish and Wildlife, generously allowed me access to unpublished data on *Gulo*. George Krochak, Registrar, American Museum of Natural History, was particularly adept at the art of the invoice. Chip Clark, Office of Exhibits, Smithsonian Institution, was a great source of photographic advice. Childs Frick initially identified most of the *Plesiogulo* material in his collection. I would also like to thank the many members, past and present, of the American Museum of Natural History Department of Vertebrate Paleontology and of the Frick Laboratory, who have contributed to the identification of the largest sample of *Plesiogulo* in the Western Hemisphere. Such well curated collections greatly enhance the productivity and pleasure of visiting researchers. This paper is an outgrowth of research undertaken in partial fulfillment of the doctorate degree at the University of Kansas. The preliminary research was supported in part by National Science Foundation Grant DEB77-15869. The manuscript was critically read and considerably improved by Earl E. Manning, Henry Galiano, Robert J. Emry, and Gary Morgan.

Systematics

The following hierarchic classification is used in this report:

Order CARNIVORA Bowdich, 1821
Family MUSTELIDAE Swainson, 1835
Subfamily MELLIVORINAE Gill, 1872
Tribe Gulonini Webb, 1969
Genus *Plesiogulo* Zdansky, 1924

Plesiogulo marshalli (Martin, 1928)

FIGURES 2, 3, 7–12

Brachypsalis marshalli Martin, 1928:233, pl. 20.
Plesiogulo marshalli.—Hibbard, 1934:247.

HOLOTYPE.—KUVP 3464, right ramus with $P_{3,4}$, M_1, and alveoli of I_2-P_2 and M_2 and skull fragments bearing glenoid fossae (Figure 2*a–c*).

TYPE LOCALITY.—Edson Quarry, NW 1/4 SE 1/4 Sec. 25, T10S, R38W, Sherman County, Kansas.

REFERRED SPECIMENS.—From the type locality: KUVP 3465, right P^4-M^1; KUVP 3467, right juvenile ramus with dP_{3-4}, M_{1-2}; KUVP 3606, right juvenile ramus with C_1, dP_4, M_1; F:AM 49479, associated right and left juvenile rami with

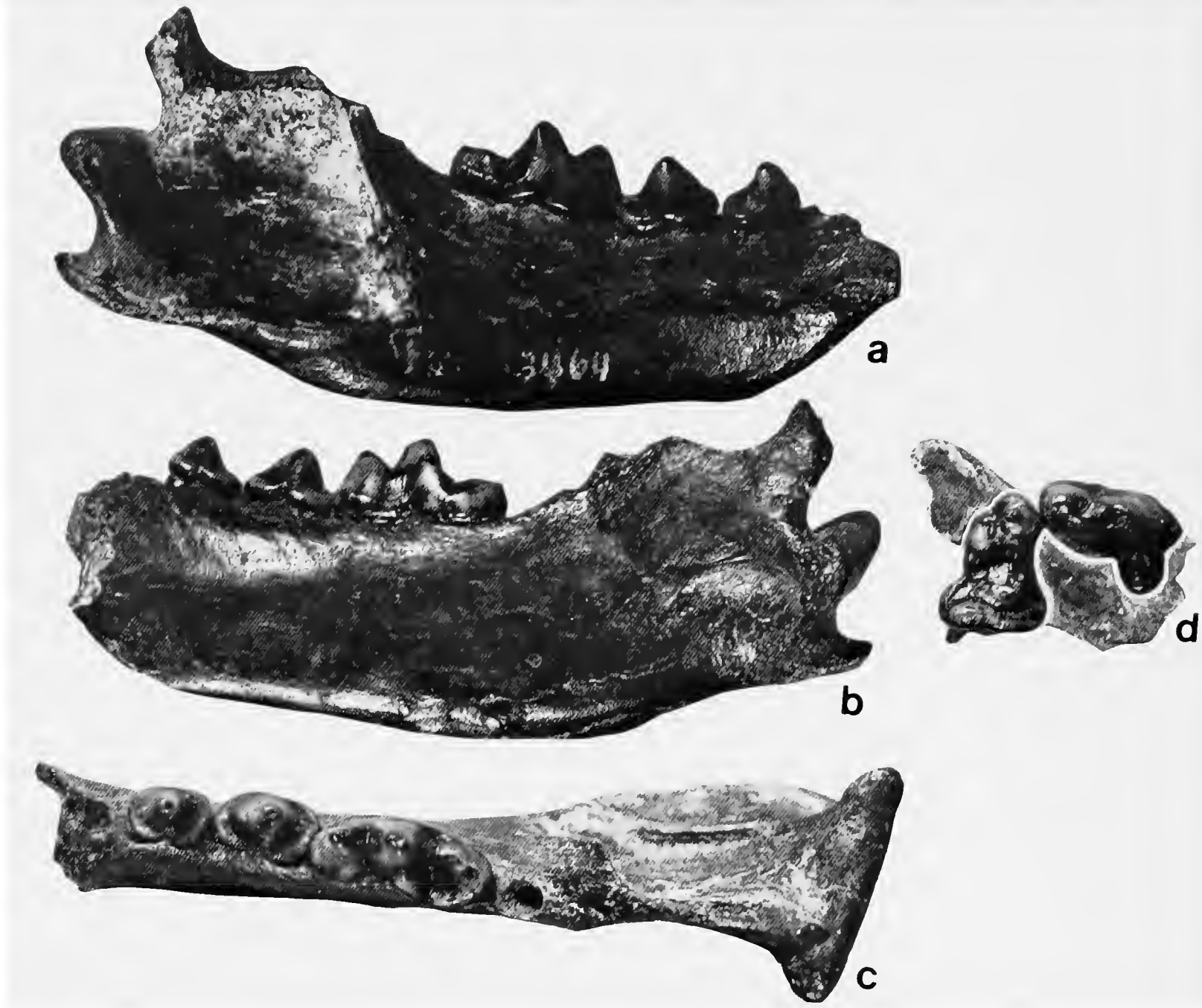

FIGURE 2.—*Plesiogulo marshalli*: *a–c*, KUVP 3464, holotype, right ramus, lateral, medial, and occlusal views; *d*, KUVP 3465, right P^4-M^1, occlusal view. (Specimens from Edson Quarry; × 1.)

right C_1-P_2, dP_4, P_4 (germ), M_1 and left C_1-P_2, dP_3; F:AM 104724, left C_1; F:AM 67650A, partial right humerus.

From Optima (Guymon), Texas County, Oklahoma: F:AM 49497, crushed skull with both rami and partial right radius; F:AM 49490, left maxilla with I^{2-3}, P^3-M^1; F:AM 49492, right P^4; F:AM 49491, right ramus with C_1-M_1; F:AM 49494, right ramus with P_3-M_2; F:AM 49493, right ramus with P_3-M_1; F:AM 49499, right ramal fragment with P_{2-4}; F:AM 49495, right ramal fragment with P_4-M_1; F:AM 49498, left ramal fragment with P_4-M_1; F:AM 49496, right ramal fragment with M_1; F:AM 67918N, partial left radius.

From Coffee Ranch, Hemphill County, Texas: TMM 41261-12, left M^1; MU 11523, right M^1; MU 5132, partial right M_1; UCMP 31944, left C^1; UCMP 31942, right P_4; UCMP 31833, right ramal fragment with P_4-M_1; UCMP 30180, right M_1; F:AM 108062, crushed skull; F:AM 23386, left maxilla with 1^{1-2}, C^1, P^2-M^1; F:AM 23387, right maxilla with P^2-M^1; F:AM 23378, right

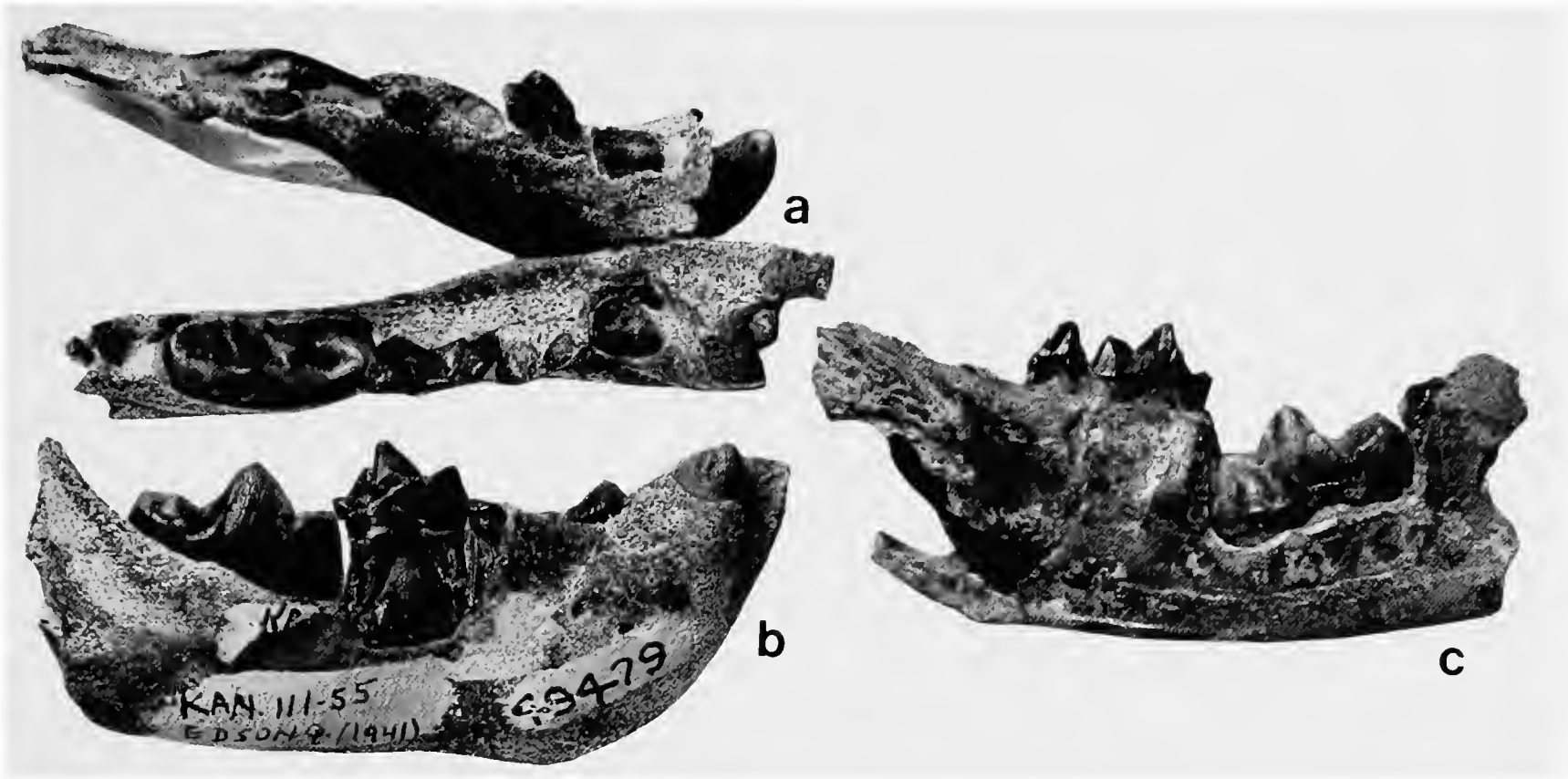

FIGURE 3.—*Plesiogulo marshalli*: *a*, *b*, F:AM 49479, right and left juvenile rami, occlusal and lateral views, teeth in "*b*" are tip of C_1, P_2, roots of dP_3, dP_4 atop P_4, and M_1; *c*, KUVP 3467, right juvenile ramus, medial view, teeth are dP_{3-4}, M_{1-2}. (Specimens from Edson Quarry; × 1.)

partial maxilla with P^3-M^1; F:AM 23379, left partial maxilla with P^3-M^1; F:AM 23378A, left P^4; F:AM 23378B, left M^1; F:AM 22270, right ramal fragment with P_{2-4}; F:AM 23388, right ramal fragment with P_3-M_1; F:AM 108052, possibly associated left humerus and ulna.

From Modesto Reservoir, Stanislaus County, California: LACM 61696, left ramus with C_1-M_1.

From McKay Reservoir, Umatilla County, Oregon: UOMNH F-3656, right maxilla fragment with P^4-M^1; UOMNH F-2441, right partial M_1.

From Ordance (Westend Blowout), Umatilla County, Oregon: two partial maxillae and an isolated M_1.

From San Juan Quarry, Rio Arriba County, New Mexico: F:AM 49230, right maxilla fragment with P^4-M^1.

From Upper Bone Valley, Polk County, Florida: UF 19253, right maxilla fragment with P^4-M^1; UF 19295, left M^1.

From White Cone, Navajo County, Arizona: USNM 244492, right M^1.

From Lost Quarry, Wallace County, Kansas: KUVP 12433, right P^4

REVISED DIAGNOSIS.—Martin (1928) did not diagnose his new taxon, *Brachypsalis marshalli*, nor did Hibbard (1934) discuss his own rationale for transferring *marshalli* to *Plesiogulo*. However, such characters in the type specimen as a relatively large M_1 with a broadened talonid, lack of a parastyle on P^4, absence of M^2, and presence of an auditory meatal spout clearly remove the species from *Brachypsalis* (Figure 2). The following diagnosis is offered for *Plesiogulo marshalli*: A North American species far larger than the Old World genotypic species, *P. brachygnathus*, and generally exceeding in size the Old World species, *P. crassa*; *Plesiogulo marshalli* differs from both Old World species in having a heavier, more massive dentition with a greater ratio of width to length for individual teeth, a larger protocone on P^4, and more pronounced cingula.

DESCRIPTION.—The following section pertains to undescribed material from Edson (for addi-

tional data on the type ramus and P^4-M^1, see Martin, 1928). Martin maintained that all of the *Plesiogulo* specimens that he described from Edson probably belonged to the same individual. Correspondence in size and occlusal surfaces supports the association of the maxilla fragment bearing P^4-M^1 (KUVP 3465) with the type ramus; however, the smooth, noncrenulated enamel of the right C^1 (KUVP 3469) precludes its referral to *Plesiogulo*. This specimen should instead be referred to *Osteoborus cyonoides*, a borophagine canid, also present in the Edson Local Fauna.

Based on the broken alveolus in the type ramus, Martin described C_1 of *Plesiogulo* to be of great size and out of proportion to the rest of the teeth. However, the alveolus is large in order to accommodate the posteriorly expanded area at the base of the crown. The canine itself is formidable, but not grossly disproportionate for a carnivore of this size. It falls far short of the astonishing canine development observed in many of the Felidae. As Martin (1928:234) stated, the M_1 talonid is indeed well developed; however, its antero-internal surface is not "deeply basined," but only slightly concave and inclined lingually. In unworn specimens the M_1 talonid is almost flat, although still inclined.

Three lower jaws (KUVP 3467 and 3606 and F:AM 49479) from Edson represent the only known deciduous dentitions of *Plesiogulo* from either Old or New World localities (Figure 3). These specimens considerably enhance our knowledge of the genus. Each of the three jaws has an alveolus indicating that a very small, single-rooted tooth was closely appressed and situated slightly lingual to the anterior end of dP_2 in juveniles and P_2 in adults. There is no indication of a tooth germ beneath any of these alveoli. Slaughter, Pine, and Pine (1974:115) state that only a single tooth ever develops in the premolar one position except in *Tapirus* and possibly certain hyraxes. Hence, the tooth associated with the aforementioned alveolus is herein referred to as dP_1. The condition of this tooth in the type of *P. marshalli* is not known because the appropriate portion of the ramus is missing; however, both dP_1 and dP^1 alveoli are present in all of the referred specimens in which this portion of the ramus or maxilla is preserved. Several specimens of *P. crassa* from the Paote localities contain dP_1 in situ.

C_1, P_2, and M_2 are also missing from the type but just emerging in juveniles F:AM 49479 and KUVP 3467. C_1 is large, although, as stated previously, not unusually so. The enamel is crenulated and a ridge extends from the basal cingulum to the tip of the crown on the antero-internal surface. P_2 is oval and double-rooted with a single blunt cusp situated towards the anterior end of the tooth. A low crest connects this cusp with the anterior and posterior borders of the crown. M_2 is a small, rounded button placed well up on the ascending ramus. A low transverse crest connects the two small lingual and labial cingular cusps.

The lower cheekteeth erupt in the following order: dP_1, dP_2, dP_3, dP_4, M_1, M_2, P_2, P_3, P_4. In the Edson juveniles, DP_2 is not preserved, but alveoli indicate a double-rooted tooth smaller than dP_3. DP_3 is a slender tooth with a high central cusp, a small accessory cusp on the antero-internal cingulum, and a posterior cingular shelf. Predictably, DP_4 foreshadows the morphology of M_1; however, the paraconid-protoconid notch is more open, the metaconid is larger, and the talonid is shorter and narrower than in M_1. The enamel of the deciduous dentition is not so heavily crenulated as that of the permanent dentition.

The three juveniles from Edson are very close in age. All have dP_4 in place and slightly worn with M_1 just emerging and unworn. In KUVP 3467 and 3606 the tip of P_2 is just visible through the alveoli of dP_2. In the third ramus, F:AM 49479, the thin bone has been chipped away to expose the unworn P_2. A slightly worn dP_3 is present in both KUVP 3467 and F:AM 49479. The canine is just emerging in F:AM 49479 and KUVP 3606, and in the latter specimen the terminus of the root of dC_1 remains closely appressed to C_1.

It seems likely that these three juveniles were litter mates; moreover, there is no evidence to

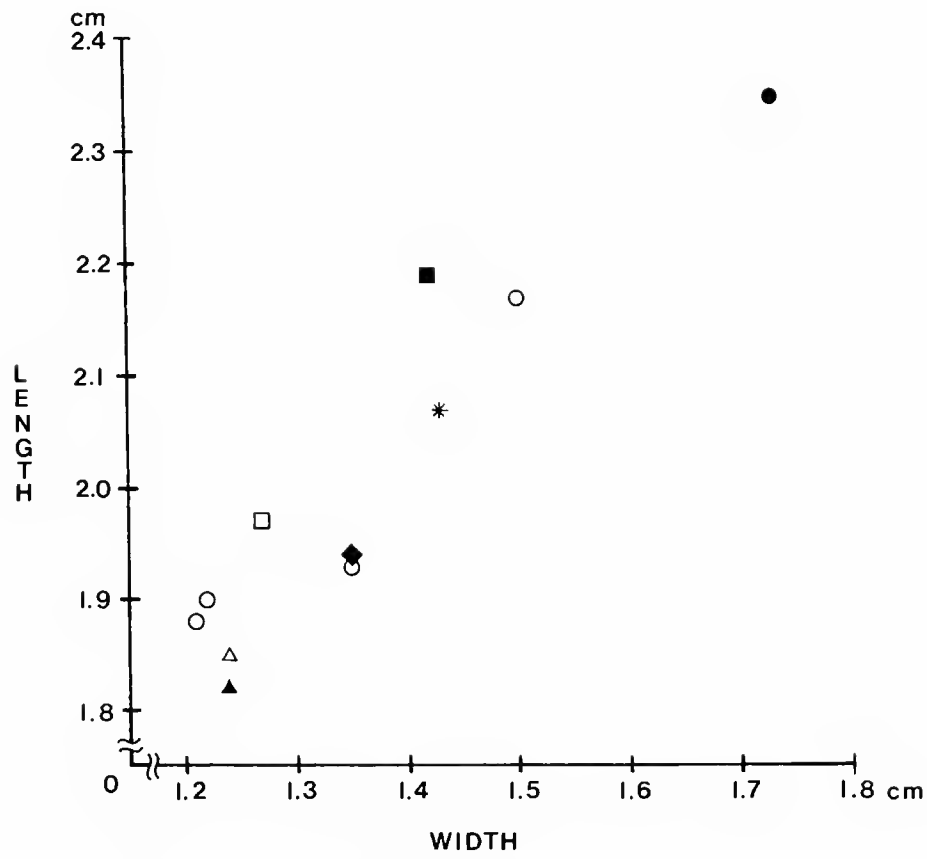

FIGURE 4.—Scatter diagram of P^4's of *Plesiogulo* from North America.

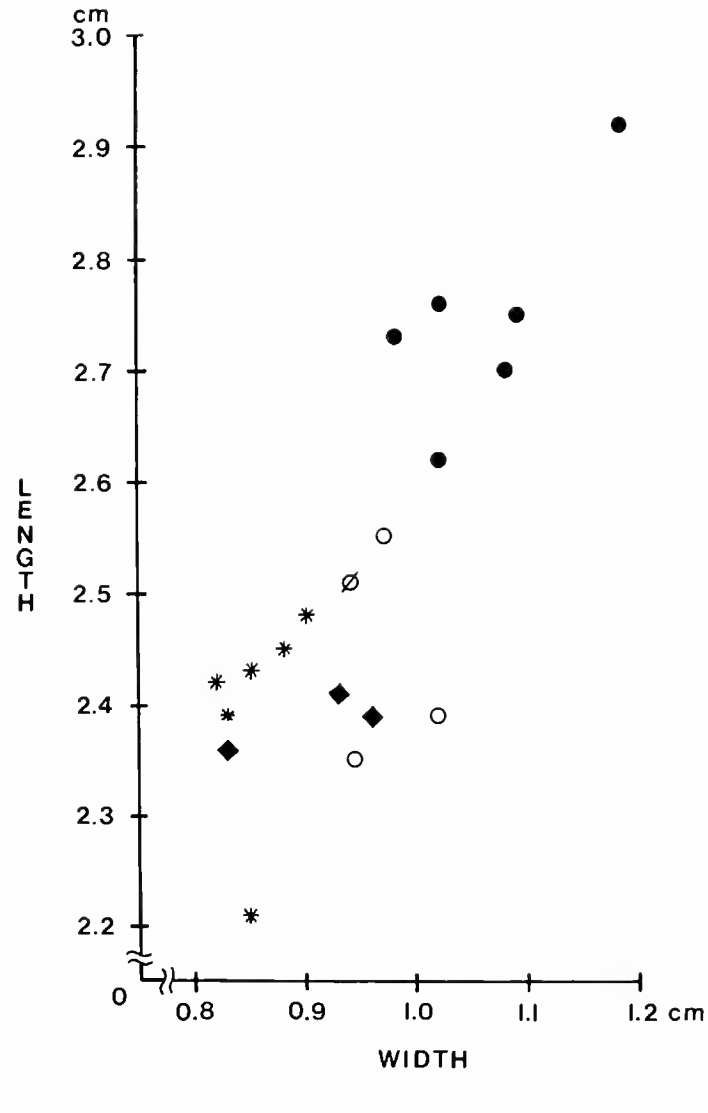

FIGURE 5.—Scatter diagram of M_1's of *Plesiogulo* from North America.

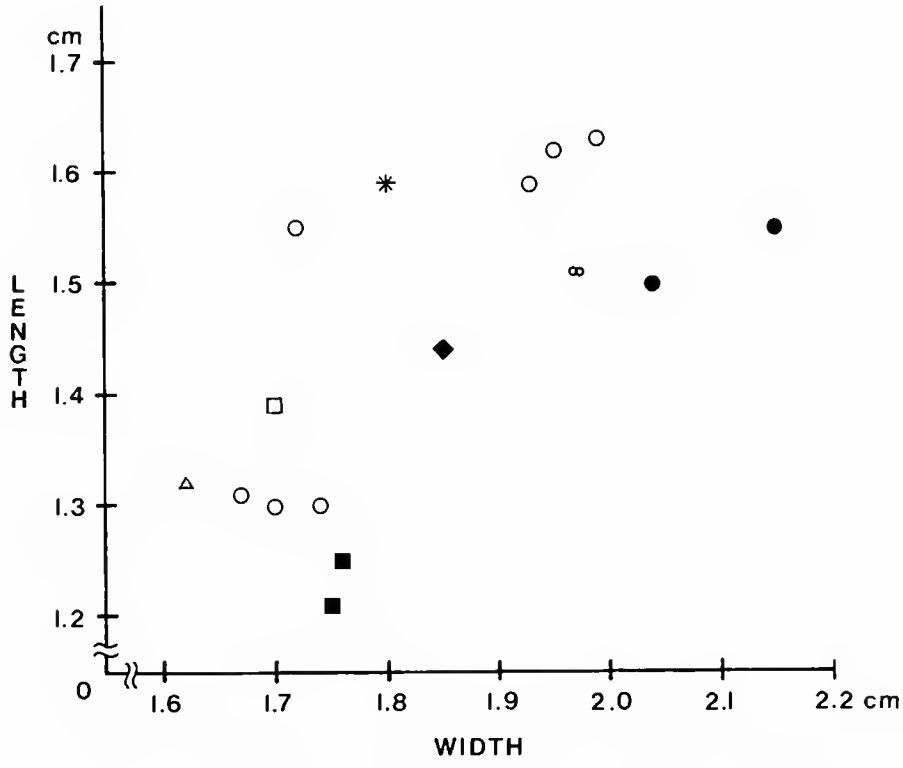

FIGURE 6.—Scatter diagram of M^1's of *Plesiogulo* from North America.

SYMBOLS FOR FIGURES 4, 5, & 6

◆ Edson	■ Bone Valley
✳ Optima	△ San Juan Quarry
○ Coffee Ranch	▲ Lost Quarry
□ McKay Reservoir	● Wikieup
⚮ Old Cabin Quarry	⌀ Modesto Reservoir

TABLE 2.—Measurements (cm) of *Plesiogulo marshalli* from Edson Quarry (O.R. = observed range, $\bar{X}$ = sample mean)

Element		*No.*	*O.R.*	$\bar{X}$
P^4	length	1	1.94	
	width at protocone	1	1.35	
M^1	length, lingual	1	1.44	
	length, median	1	0.99	
	width	1	1.85	
P_2	length	1	0.73	
	width	1	0.57	
P_3	length	1	1.10	
	width	1	0.76	
P_4	length	1	1.36	
	width	1	0.85	
M_1	length	3	2.36–2.41	2.39
	width at talonid	3	0.83–0.96	0.90
M_2	length	1	0.66	
	width	1	0.60	
P_3-M_1	length	1	4.77	
Condylar	width	1	3.29	
	length	2	0.83–0.90	
dP_3	width	2	0.45–0.50	
	length	3	1.42–1.43	1.43
dP_4	width	3	0.60–0.67	0.63

TABLE 3.—Measurements (cm) of *Plesiogulo marshalli* from Optima (O.R. = observed range, $\bar{X}$ = sample mean, s.d. = standard deviation)

Element		*No.*	*O.R.*	$\bar{X}$	*s.d.*
I^3	length	1	0.91		
	width	1	0.84		
P^3	length	1	1.16		
	width	1	0.80		
P^4	length	2	2.07–2.11		
	width	1	1.43		
M^1	length, lingual	1	1.59		
	length, median	1	0.83		
	width	1	1.80		
C_1	length	1	1.52		
	width	1	1.05		
P_2	length	3	0.72–0.77	0.74	
	width	3	0.51–0.55	0.53	
P_3	length	5	0.91–1.01	0.95	0.05
	width	5	0.61–0.72	0.65	0.04
P_4	length	7	1.23–1.44	1.31	0.08
	width	7	0.73–0.87	0.79	0.05
M_1	length	6	2.21–2.48	2.40	0.10
	width at talonid	7	0.82–0.90	0.86	0.03
M_2	length	2	0.72–0.77		
	width	2	0.62–0.65		
C_1-M_1	length	1	7.04		
Radius	length	1	12.32		
	width, proximal	1	1.79		

indicate that the only adult *Plesiogulo* at Edson was not a female. The young of *Gulo*, usually numbering two or three, remain with their mother for about two years (Walker, 1964). A female with her litter of cubs seems the most logical explanation of the unusual sample of *Plesiogulo* found in the Edson Local Fauna (Table 2).

DISCUSSION.—Specimens of *Plesiogulo marshalli* from nine localities are discussed in relation to the holotypic and referred material of *P. marshalli* from Edson. The problems inherent in comparing small samples and, in many cases, isolated teeth are all too familiar. Too often is individual variation interpretated as variation at the specific level. Fortunately, the very large sample of *P. crassa* from Asia (Zdansky, 1924; Kurtén, 1970) provides considerable insight into the amount of variation present in a related species.

Scatter diagrams (Figures 4–6) illustrate the size variation in the three most generically distinct teeth of *Plesiogulo*: P^4, M^1, and M_1. Fortunately, these teeth were also among the most numerous in the total North American sample (P^4 = 11, M^1 = 16, M_1 = 17). The upper and lower carnassials (Figures 4, 5) proved to be the most diagnostic at the specific level. M^1, especially the length of the lingual lobe, was the most variable of all the cheek teeth (Figure 6).

The sample from Optima contains only one partial maxilla in addition to a badly crushed partial skull; the remaining specimens are lower dentitions (Figure 7, Table 3). There are no upper incisors or P^3 from the type locality to compare with those from Optima; however, these teeth, and the rest of the Optima sample do compare well with dentitions from Coffee Ranch. The P^4 from Optima is slightly larger with the anterior notch slightly deeper than the P^4 from Edson. In the Optima M^1 the inner lobe is slightly longer than in the Edson M^1. None of the several partial rami and ramal fragments from Optima differ

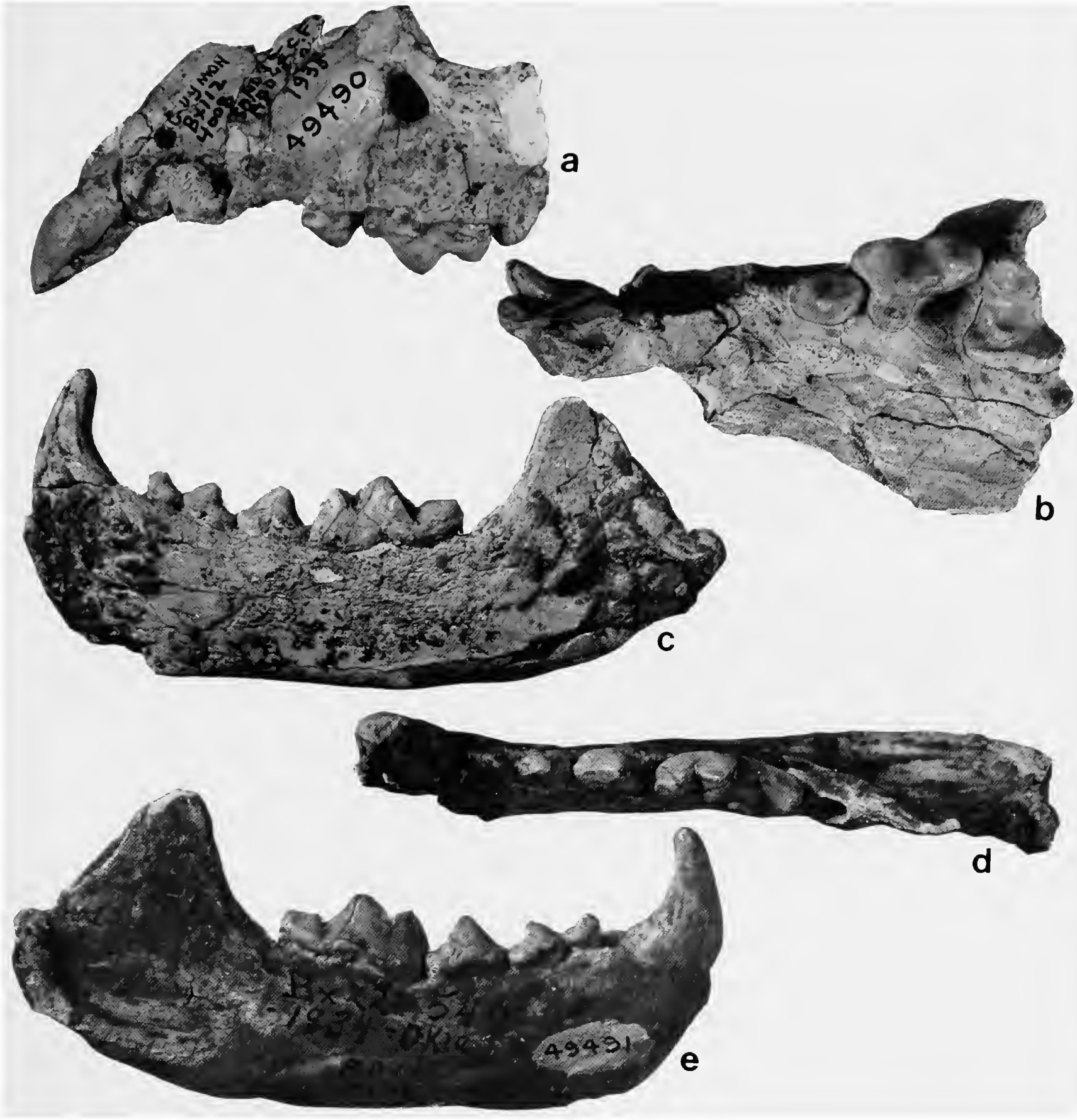

FIGURE 7.—*Plesiogulo marshalli*: *a*, *b*, F:AM 49490, left maxilla, lateral and occlusal views; *c*–*e*, F:AM 49491, right ramus, medial, occlusal, and lateral views. (Specimens from Optima; × 1.)

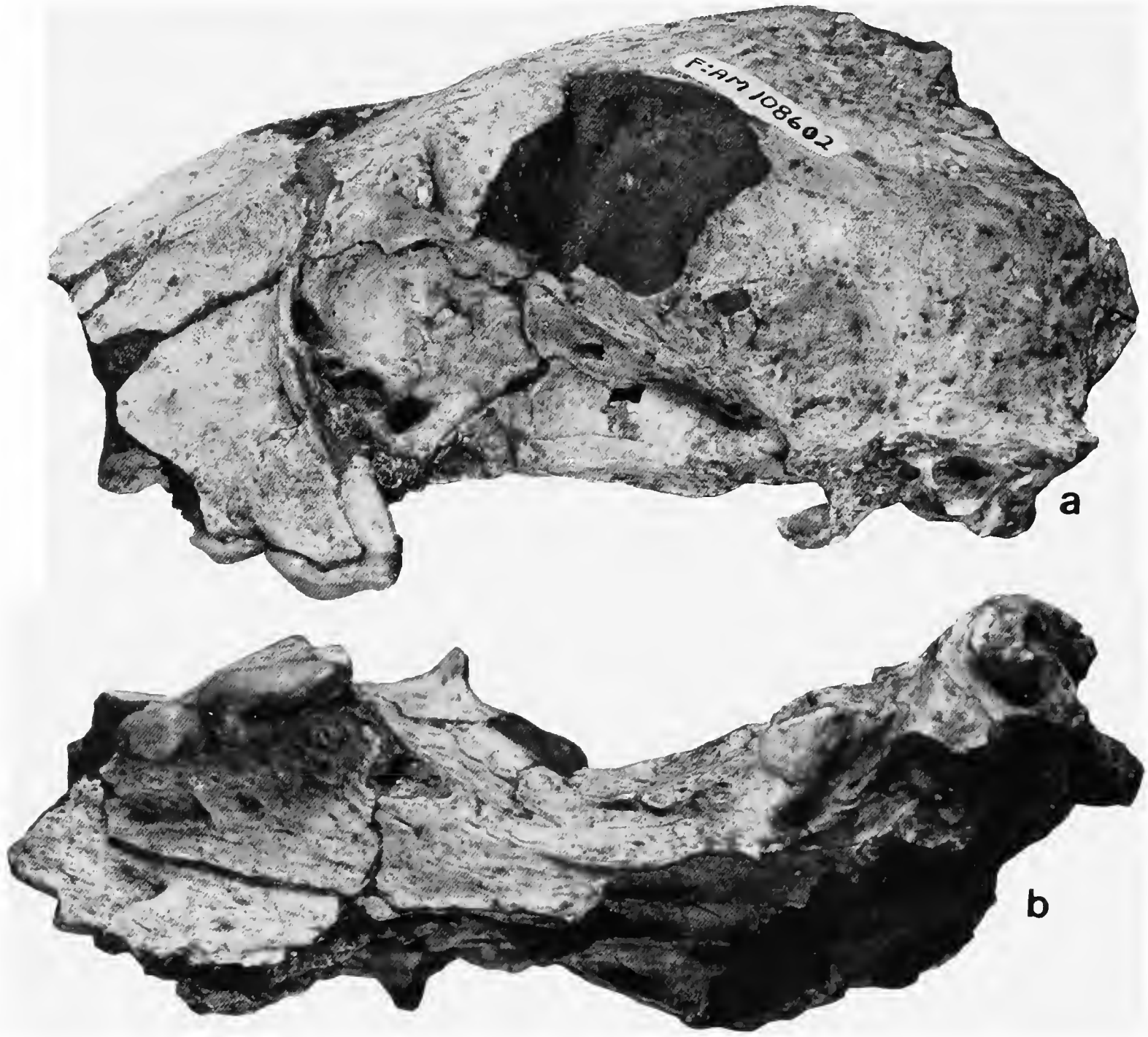

FIGURE 8.—*Plesiogulo marshalli*, F:AM 108602, partial skull: *a*, lateral view; *b*, occlusal view. (Specimen from Coffee Ranch; × 1.)

significantly from the type ramus. The C_1 from Optima is slightly smaller than the isolated C_1 from Edson. The P_{3-4} and M_1 from Optima compare well with those from Edson. The Optima sample contains the only other M_2's (F:AM 49494 and 49497) from a New World locality; they are slightly larger than the M_2 from Edson.

The Coffee Ranch sample bears an even closer resemblance to the type material than that of Optima. The ratio of upper to lower dentitions is the reverse of the Optima sample; Coffee Ranch contains nine partial upper dentitions, but only two lowers. The partial skull, F:AM 108062 (Figure 8, Table 4) from Coffee Ranch is far from complete, although not so badly damaged as the one from Optima. These two specimens, in addition to the fragments from Edson, constitute the only cranial material known for *P. marshalli*. The skull is least damaged on the left side; the remaining teeth are worn left P^{3-4}. The left infraorbital canal is intact; it is larger and more rounded than in *Gulo* and situated above the

TABLE 4.—Measurements (cm) of *Plesiogulo marshalli* from Coffee Ranch (O.R. = observed range, $\bar{X}$ = sample mean, s.d. = standard deviation)

Element		*No.*	*O.R.*	$\bar{X}$	*s.d.*
C^1	length	2	1.22–1.35		
	width	1	0.97		
P^2	length	2	0.80–0.82		
	width	2	0.57–0.59		
P^3	length	4	1.11–1.29	1.17	0.08
	width	4	0.66–0.80	0.72	0.06
$P^{4\,1}$	length	5	1.85–2.17	1.95	0.13
	width	4	1.21–1.50	1.32	0.14
M^1	length, lingual	7	1.30–1.63	1.47	0.16
	length, median	7	0.84–1.03	0.92	0.08
	width	7	1.67–1.99	1.81	0.14
C^1-M^1	length	1	6.54		
P_3	length	2	1.03–1.04		
	width	2	0.73–0.75		
P_4	length	4	1.28–1.39	1.34	0.05
	width	4	0.76–0.88	0.81	0.05
M_1	length	3	2.35–2.54	2.42	0.10
	width at talonid	3	0.95–1.02	0.98	0.04
Humerus	length	1	15.11		
	width, distal	1	4.02		
Ulna	length	1	14.96		
	antero-posterior at coronoid	1	2.53		

TABLE 5.—Measurements (cm) of *Plesiogulo marshalli* from several localities (O.R. = observed range)

Element		*No.*	*O.R.*
MODESTO RESERVOIR			
C_1	length	1	1.53
	width	1	1.18
P_2	length	1	0.78
	width	1	0.59
P_3	length	1	1.05
	width	1	0.68
P_4	length	1	1.48
	width	1	0.90
M_1	length	1	2.51
	width at talonid	1	0.94
C_1-M_1	length	1	7.98
MCKAY RESERVOIR			
P^4	length	1	1.97
	width	1	1.27
M^1	length, lingual	1	1.39
	length, median	1	0.88
	width	1	1.70
BONE VALLEY			
P^4	length	1	2.18
	width	1	1.42
M^1	length, lingual	2	1.21–1.25
	length, median	2	0.87–0.98
	width	2	1.75–1.76
SAN JUAN QUARRY			
P^4	length	1	1.85
	width	1	1.24
M^1	length, lingual	1	1.32
	length, median	1	0.93
	width	1	1.62
LOST QUARRY			
P^4	length	1	1.82
	width	1	1.24
WHITE CONE			
M^1	length, median	1	0.83

middle of P^4 rather than the front of P^4 as in *Gulo*. Both postorbital processes are present and a low temporal crest from each extends posteriorly to form the sagittal crest. All of the muzzle anterior to P^3 is missing, as well as most of the occipital region. Part of the left parietal, mastoid process, and glenoid fossa are still present. As in *Gulo*, the optic foramen is situated 1 to 2 cm anterior to the closely appressed orbital fissure and foramen ovale. The foramen rotundum is located medial to and on a level with the glenoid fossa. The common aperature of the sphenopalatine foramen and the caudal end of the posterior palatine canal lies, as in *Gulo*, in the medial wall of the orbit at a level with the posterior end of P^4.

The P^4's from Coffee Ranch bracket the Edson P^4 in size, and one (F:AM 23386) is almost identical (Figure 9*d*, *e*). The Coffee Ranch M^1's show a wide range of variation, some approaching in size those of *P. lindsayi*, new species, and some almost as small as *P. marshalli* from Bone Valley. The lower premolars compare well with those from Edson. The single M_1 is very close in length to the Edson M_1's, although very slightly wider across the talonid (Figure 9*a–c*).

The single specimen of *P. marshalli* from Modesto Reservoir (LACM 61696) is a left ramus

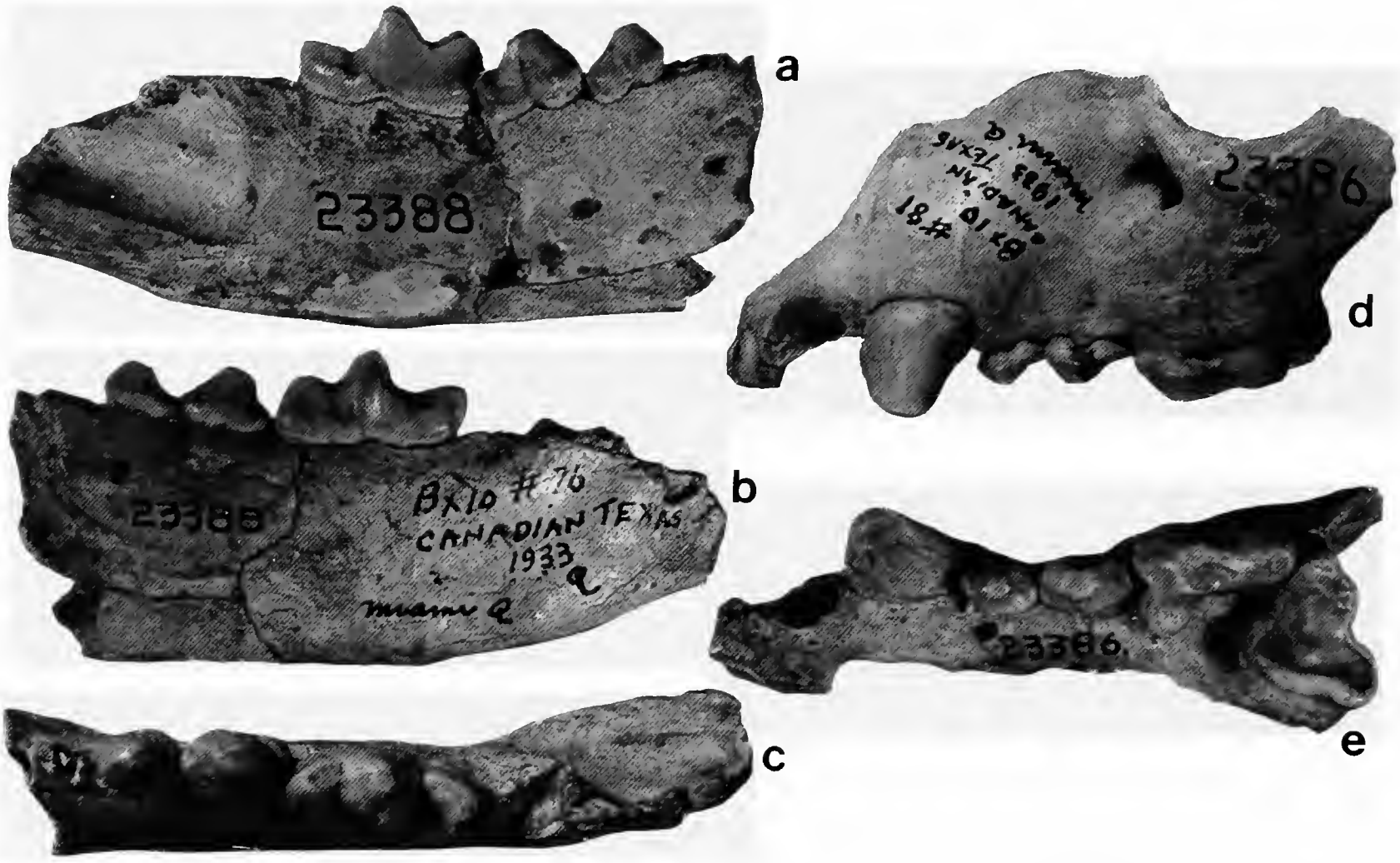

FIGURE 9.—*Plesiogulo marshalli*: *a–c*, F:AM 23388, right ramus, lateral, medial, and occlusal views; *d*, *e*, F:AM 23386, left maxilla, lateral and occlusal views. (Specimens from Coffee Ranch; × 1.)

bearing C_1, P_{2-4}, and M_1 (Figure 10*g–i*). The cheek teeth exhibit very little wear and indicate a mature individual somewhat younger than the type specimen. C_1 and P_2 compare well with those in an Edson juvenile (F:AM 49479) (Figure 3*a*, *b*). Although broken, C_1 still exhibits part of the antero-internal ridge as well as crenulated enamel. The enamel of the cheek teeth is not so strongly crenulated as that of C_1. An alveolus for dP_2 separates C_1 and P_2. The longitudinal crests of P_{2-4} are more pronounced than in the Edson specimens, and P_3-M_1 resemble very closely those of the type ramus. Two very small depressions indicate the position of the M_2 alveolus, which had commenced closure sometime during the life of this individual.

The right maxilla fragment bearing P^4-M^1 and a possibly associated partial M_1 of *P. marshalli* from McKay Reservoir (Figure 10*a*, Table 5) are very close in size and morphology to those from Edson (Table 2). There is a high degree of correspondence even in such features as the internal cingulum and the two anterior ridges on P^4 and the occlusal outline of M^1, an extremely variable tooth. Two undescribed partial maxillae from nearby Ordnance are probably referable to *P. marshalli* (J. E. Martin, pers. comm.).

An isolated right M^1 is the only specimen of *Plesiogulo* from White Cone (Figure 10*b*, Table 5). The external end of the tooth, including most of the paracone and metacone, is missing, as are fragments of enamel all along the posterior edge of the crown. The tooth compares well with the Edson M^1 in size, placement of the paracone, metacone, and protocone, and extent of the median constriction. The hypocone is not quite so widely expanded as in the Edson M^1, and the internal border is more strongly concave. How-

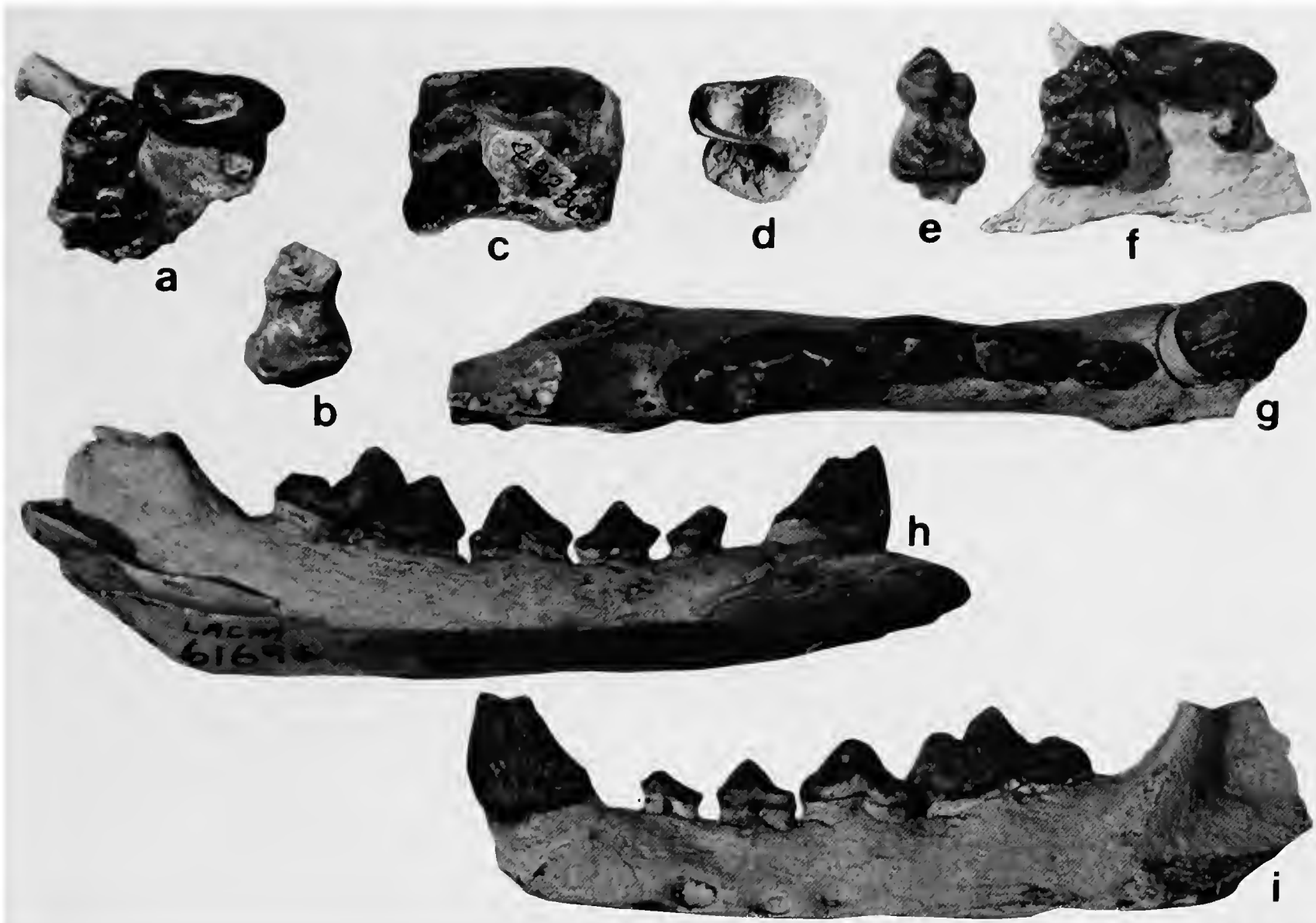

FIGURE 10.—*Plesiogulo marshalli*: *a*, UOMNH F-3656, right P^4-M^1, occlusal view, specimen from McKay Reservoir; *b*, USNM 244492, right M^1, occlusal view, specimen from White Cone; *c*, F:AM 49230, right P^4-M^1, occlusal view, specimen from San Juan Quarry; *d*, KUVP 12433, right P^4, occlusal view, specimen from Lost Quarry; *e*, UF 19295, left M^1, occlusal view, specimen from Bone Valley; *f*, UF 19253, right P^4-M^1, occlusal view, specimen from Bone Valley; *g–i*, LACM 61696, cast of left ramus, occlusal, medial, and lateral views, specimen from Modesto Reservoir. (× 1.)

ever, since these discrepancies are most probably due to individual variation, I have herein referred the White Cone specimen to *P. marshalli*.

Three localities have produced a few isolated teeth of *P. marshalli,* which are somewhat smaller and more slender than material from the preceding localities (Figure 10, Table 5). The sole specimen from Lost Quarry is the smallest P^4 in the total *P. marshalli* sample. The San Juan Quarry material consists of a right maxilla fragment bearing P^4-M^1. This P^4 is almost as small as that from Lost Quarry and, like it, bears a slightly reduced protocone. An associated right P^4-M^1 and an isolated left M^1 have been recovered from Bone Valley. This P^4 is one of the largest in the total sample; the M^1's, however, are the smallest such teeth. The two Bone Valley M^1's compare well with the San Juan Quarry M^1; moreover, three M^1's from Coffee Ranch (not illustrated) closely approach these teeth in size. There is more than sufficient overlap in both size and morphology between the material from San Juan Quarry, Bone Valley, and Lost Quarry and the material from Edson, Optima, and Coffee Ranch to warrant its referral to *P. marshalli*.

To date, no postcranial elements of *Plesiogulo*

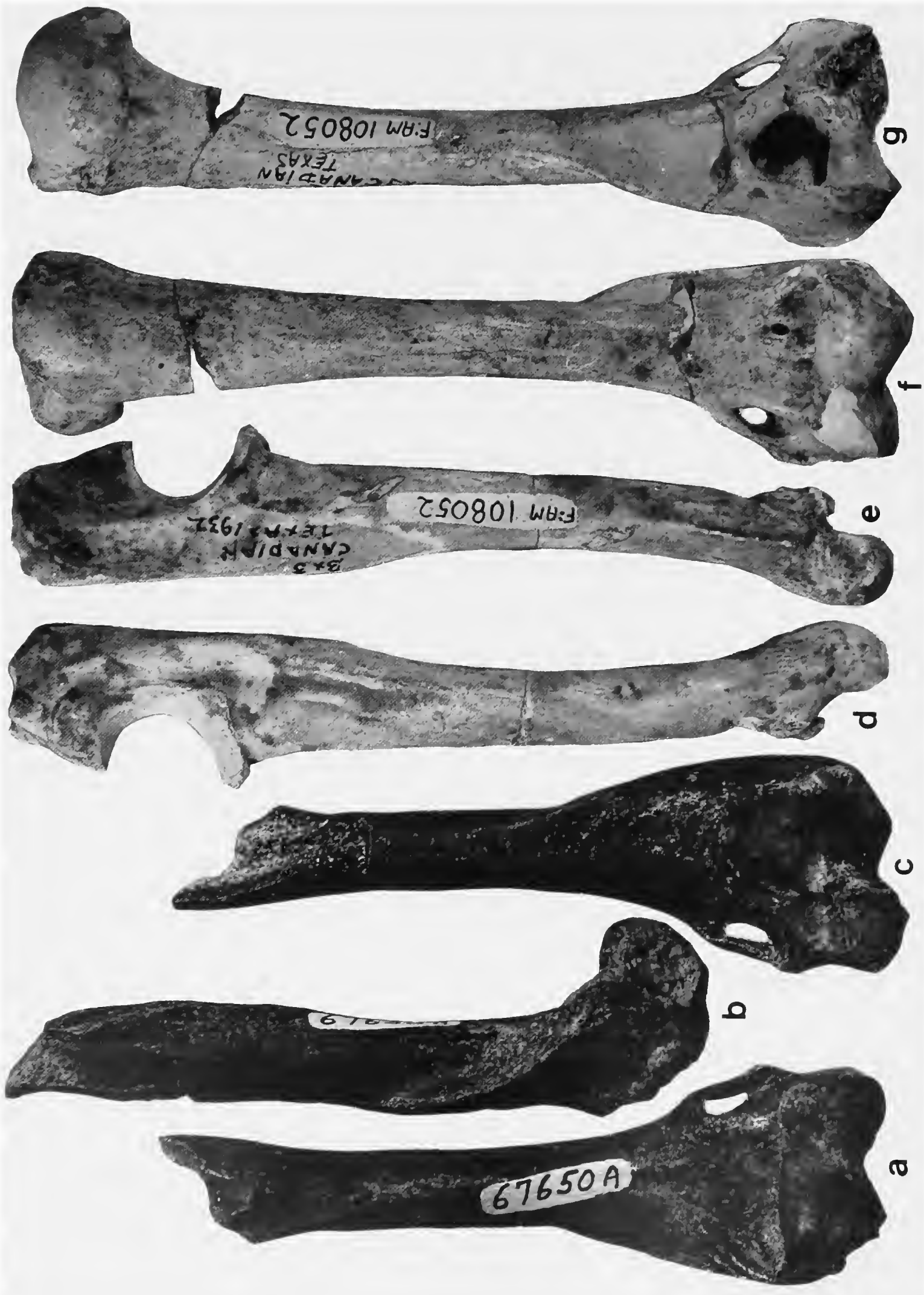

FIGURE 11.—*Plesiogulo marshalli*: *a–c*, F:AM 67650A, right humerus, anterior, lateral, and posterior views, specimen from Edson Quarry; *d*, *e*, F:AM 108052, left ulna, lateral and medial views, specimen from Coffee Ranch; *f*, *g*, F:AM 108052, left humerus, anterior and posterior views, specimen from Coffee Ranch. (× 1.)

FIGURE 12.—*Plesiogulo marshalli*: *a*, *b*, F:AM 49497, right radius, anterior and posterior views; *c*, *d*, F:AM 67918N, left radius, anterior and posterior views. (Specimens from Optima; × 1.)

have been described in the New World literature; however, Hendey (1978) briefly described some postcrania from Langebaanweg, South Africa, and referred them to *P. monspessulanus* Viret. I have herein referred five specimens to *P. marshalli*, a partial left humerus from Edson, a possibly associated left humerus and ulna from Coffee Ranch, and two partial radii from Optima. These elements were not found in direct association with dentitions, but their size is compatible with estimates of body size in *Plesiogulo* and in many characters their morphology is suggestive of *Gulo*. Moreover, these elements clearly do not belong to any other genera in their respective faunas. *Osteoborus cyonoides* is the only carnivore present in these faunas with postcrania similar in size to those of *Plesiogulo*, although most adult *Osteoborus* skeletal elements are somewhat larger.

The Edson humerus is complete distal to the tip of the deltopectoral rugosity, except for fragments from the lateral and medial epicondyles (Figure 11*a–c*). The Coffee Ranch humerus is complete but for a fragment of the medial epicondyle (Figure 11*f*, *g*). The two humeri are very close in size, and both bear a large entepicondylar (supracondyloid) foramen, which is not present in *Osteoborus*. The humeral shaft, especially the proximal half, is straighter in *Plesiogulo* than in *Osteoborus*. The medial epicondyle in *Plesiogulo* is much smaller than in *Gulo* or *Osteoborus*, resulting in a proportionately narrower distal end. The olecranon fossa is larger and more deeply excavated in *Plesiogulo* than in *Gulo*.

The only ulna is from Coffee Ranch and is missing only a few small chips of bone (Figure 11*d*, *e*). Its shaft is not so long and slender as in *Osteoborus*, but considerably heavier than in *Gulo*. The olecranon process is longer and more concave medially in *Plesiogulo* than in *Gulo* and bears an elongate groove in its top. The roughened area for the attachment of the interosseous ligament is much larger in *Plesiogulo* than in *Gulo* and extends farther up the shaft than in *Osteoborus*. The styloid process of the ulna is heavier and more rounded in *Plesiogulo* than in *Osteoborus*. This structure is also heavy in *Gulo*, but tends to be flattened distally rather than rounded as in *Plesiogulo*. The crest on the posteromedial face of the distal end is much sharper in *Gulo* than in *Plesiogulo*.

Two radii, one right and one left, are present in the Optima sample (Figure 12). The right radius is missing half of the proximal articular surface, and its distal end is badly crushed. The left radius is missing only the distal articular surface. Radii of adult *Osteoborus* are almost always longer and heavier than those of *Plesiogulo*. The outline of the proximal articular surface is pointed in *Plesiogulo* as opposed to rounded in *Osteoborus*. The bicipital (radial) tuberosity for the

insertion of m. biceps is a raised, rough area bordered by a curving lateral crest in *Plesiogulo*; an additional medial crest is present in *Gulo*. In *Osteoborus* this feature is a large, knob-like process. *Plesiogulo* has a deep groove on the lateral face of the distal end. This groove is shallow in *Osteoborus* and very shallow in *Gulo*. The crest forming the posterior border of this groove is sharper in *Plesiogulo* than in *Osteoborus*.

The limbs of *Plesiogulo* are generally comparable to those of *Gulo*. The ratio of the lengths of proximal to distal elements is approximately the same and does not suggest a marked difference in degree of cursoriality. Both wolverines possess distal elements that are far shorter than those of *Osteoborus*, which conforms to the long-legged canid norm. When compared to corresponding bones of compariable size in *Gulo*, the greater size and rugosity of muscle attachments on the radius and ulna of *Plesiogulo* suggest that the latter genus had the more powerful antebrachium.

Plesiogulo lindsayi, new species

FIGURES 13–16

HOLOTYPE.—F:AM 49384, muzzle bearing right I^1-M^1 and left I^{2-3}, P^{2-3}, and broken P^4-M^1 (Figure 13).

TYPE LOCALITY.—Wikieup area, Mojave County, Arizona; Big Sandy Formation; late Hemphillian Land Mammal Age.

REFERRED SPECIMENS.—From the type locality: F:AM 49386, crushed palate with right I^2-C^1, P^{2-3} and left P^{2-4}; F:AM 49385, crushed palate with right I^3-C^1, P^2-M^1 and left P^2-M^1; F:AM 108053, right C^1; F:AM 108049, right P^4; F:AM 49391, right P^3; F:AM 49374, left M^1; F:AM 49392A, right M^1; F:AM 49392B, left M^1; F:AM 108054, partial left M^1; F:AM 108055, right C_1; F:AM 108056, left C_1; F:AM 108057, right C_1; F:AM 49387, left ramus with P_2-M_1; F:AM 49369, right ramus with P_2-M_1; F:AM 49389C, left P_{2-4}; F:AM 49370, left P_4-M_1; F:AM 49388, right P_4-M_1; F:AM 49390, right P_4-M_1; F:AM 108048, right P_4; F:AM 49389D, left P_4; F:AM 49373, right M_1; F:AM 49389A, partial left M_1; F:AM 49389B, left M_1; F:AM 67957, right ulna and left ischium with partial acetabulum; F:AM 67958, right radius; F:AM 67958A, right radius; F:AM 67958B, partial left radius; F:AM 105372, partial right ulna.

From Old Cabin Quarry, Pima County, Arizona: F:AM 50690, crushed palate with right P^2-M^1 and left P^3-M^1, right ramus with I_3-C_1, P_2-M_1, and left ramus with I_3-C_1, P_3-M_1.

From Redington Quarry, Pima County, Arizona: F:AM 108058, right C^1; F:AM 108059, left C_1; F:AM 108060, left ulna.

From Pinole Tuff, Contra Costa County, California: UCMP 57522, left P_4.

ETYMOLOGY.—The species is named for Everett H. Lindsay.

DIAGNOSIS.—*Plesiogulo lindsayi* compares to Old World species as follows: larger than *P. brachygnathus*, *P. minor*, *P. crassa*, and *P. praecocidens*, smaller than *P. major*, and about the same size as *P. monspessulanus*. *Plesiogulo lindsayi* differs from *P. monspessulanus* in the presence of a strong metaconid on M_1. *P. lindsayi* is larger than the only other New World species, *P. marshalli*, and differs from it in the following: I^{1-2} not as reduced; I^3 and C^1 relatively larger; superior premolars larger in relation to M^1 and more crowded; P^3 bears a lingual bulge, which is small or absent in *P. marshalli*; P^4 proportionately larger with more posteriorly placed protocone and a weak labial cingulum not present in *P. marshalli*; lingual lobe of M^1 not as expanded and with a more angular posterior corner; greater ratio of width to length in M^1; protocone of M^1 stronger and more centrally placed; ramus deeper and more massive; masseteric fossa more deeply excavated and extending beneath the M_1 talonid as opposed to beneath M_1 posterior border in *P. marshalli*; inferior premolars larger in relation to M_1; stronger lingual bulge on P_4; greater ratio of width to length in M_1; talonid broader with a higher hypoconid and mesoconid; metaconid not as tightly appressed to protoconid; M_2 alveolus smaller and not as high on the ascending ramus.

DESCRIPTION.—The type specimen, collected by Robert J. Emry, consists of the anterior portion

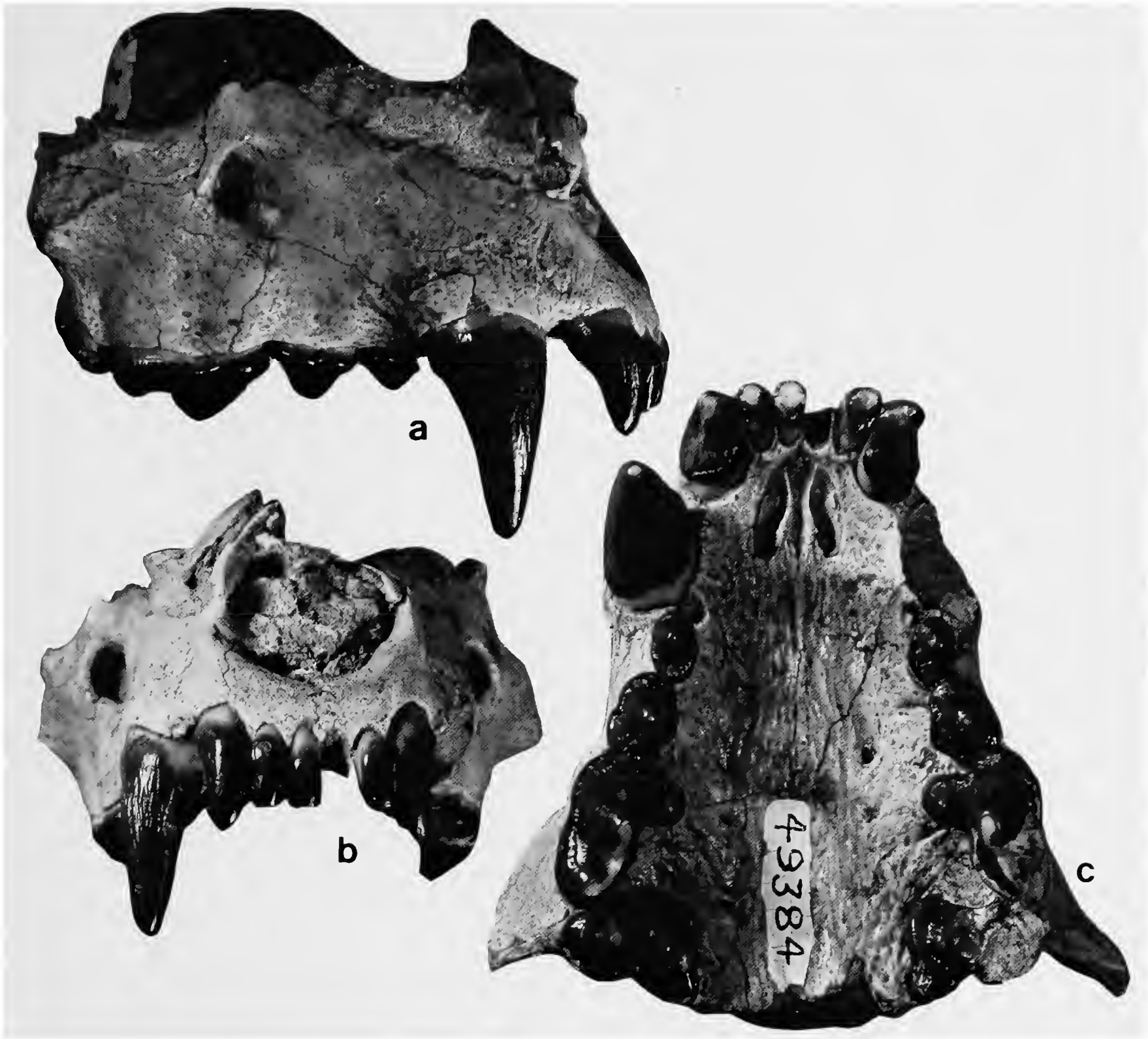

FIGURE 13.—*Plesiogulo lindsayi,* new species, holotype, F:AM 49384, partial skull: *a*, lateral view; *b*, frontal view; *c* occlusal view; specimen from Wikieup. (× 1.)

of a skull; everything posterior to M^1 is missing (Figure 13, Table 6). The nasals and most of the premaxilla are crushed, although the ventral border of the external nares, both infraorbital foramina, and both anterior roots of the zygomatic arches are intact. The section of the premaxilla bearing I^{1-3} is undamaged. The palate is complete, and the only teeth missing are left I^1, left C^1, both P^1's, and portions of left P^4-M^1.

The premaxilla is robust to accommodate the large incisors. The incisive foramina (palatine fissures) are elongate and separated by a narrow bridge of bone. The large, round infraorbital foramen is dorsal to the anterior end of P^4 The

TABLE 6.—Measurements (cm) of *Plesiogulo lindsayi*, new species, from Wikieup (O.R. = observed range, $\bar{X}$ = sample mean, s.d. = standard deviation)

Element		*No.*	*O.R.*	$\bar{X}$	*s.d.*
I^1	length	1	0.85		
	width	1	0.46		
I^2	length	1	0.92		
	width	1	0.53		
I^3	length	2	1.16–1.24		
	width	2	0.78–1.07		
C^1	length	1	1.75		
	width	1	1.39		
P^2	length	3	0.93–0.97	0.95	
	width	3	0.66–0.70	0.69	
P^3	length	4	1.21–1.39	1.30	0.08
	width	4	0.85–1.02	0.93	0.07
P^4	length	1	2.35		
	width	1	1.73		
M^1	length, lingual	3	1.33–1.55	1.46	
	length, median	4	0.94–1.02	0.97	0.15
	width	3	2.00–2.15	2.06	
C^1-M^1	length	1	7.82		
P_2	length	3	0.79–.81	0.80	
	width	3	0.64–.65	0.65	
P_3	length	3	1.04–1.13	1.09	
	width	3	0.70–0.77	0.74	
P_4	length	6	1.40–1.65	1.51	0.08
	width	6	0.87–1.01	0.93	0.05
M_1	length	7	2.49–2.92	2.71	0.13
	width at talonid	6	0.98–1.18	1.06	0.07
Ulna	antero-posterior at coronoid	2	2.47–2.56		
Radius	width, proximal	2	1.73–1.75		
	antero-posterior, proximal	3	1.00–1.13	1.08	

first and second incisors are subequal in size, but both are greatly exceeded by I^3, which is very large and caniniform. The incisiors are closely appressed, but still in alignment; their anterior surfaces form a shallow arc, rather than a straight line as in *Gulo*. A very short diastema separates I^3 from C^1. The canine is quite impressive, and its enamel is heavily crenulated; two ridges extend from the base of the crown to the tip, one on the antero-internal surface and one on the posterior surface.

Alveoli indicate a small, single-rooted dP^1. P^2 is double-rooted with a cingular shelf surrounding the blunt central cusp. The lingual root of P^3 is large, distinct from the posterior root, and produces a strong bulge in the lingual border of the crown. The tooth is surrounded by a cingulum, which lengthens into a shelf posteriorly. The upper carnassial (P^4) is very large. A ridge extends from the basal cingulum to the tip of the paracone on the anterior surface. A second ridge connecting the large protocone with the paracone is less distinct. A weak cingulum is present on the labial surface and a stronger one on the lingual surface. The width of M^1 exceeds its length, and the tooth exhibits the characteristic median constriction and expanded inner lobe. The paracone is larger and higher than the metacone, and both cusps are situated well in from the labial border. The lingual lobe of the tooth is long with an angular rather than a rounded posterior corner. The protocone is low and crescentic.

Twenty-three dentitions and isolated teeth constitute the hypodigm of *P. lindsayi* (Figure 14, Table 6). The upper dentitions closely resemble that of the type. The most complete ramus (F:AM 49382) is missing most of the coronoid process, about half of the condyle, and everything anterior to the P_3 alveolus. The body of the ramus is deep and heavy, and the deep masseteric fossa extends beneath the talonid of M_1. Neither dP_1 nor any of the lower incisors have been recovered. The lower canine, like the upper, is very large with heavily crenulated enamel. P_{2-4} are double-rooted, single-cusped teeth. P_3 and P_4 each have prominent anterior and posterior ridges extending from the basal cingulum to the tip of the single central cusp. P_4, much like P^3, has a strong bulge on the lingual side of the crown; the posterior root is quite broad. The lower carnassial is broad for its length with a strong metaconid. The talonid is wide and its flat, non-basined surface dips lingually. The only two discernible talonid cusps are the hypoconid and mesoconid. A small,

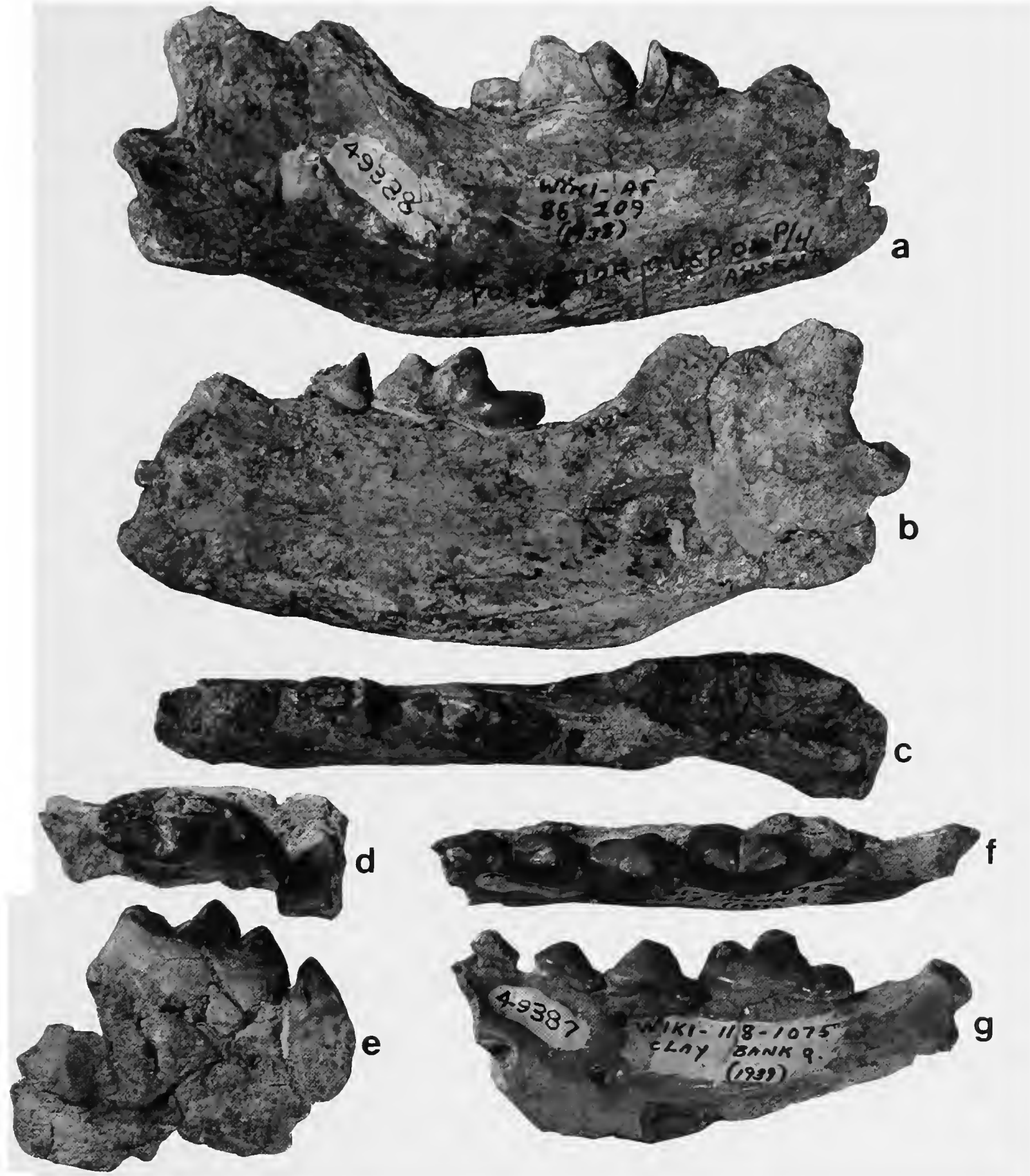

FIGURE 14—*Plesiogulo lindsayi*, new species: *a–c*, F:AM 49388, right ramus, lateral, medial, and occlusal views; *d,e*, F:AM 49370, left P^4-M^1, occlusal and medial views; *f,g*, F:AM 49387, partial left ramus, occlusal and lateral views. (Specimens from Wikieup; × 1.)

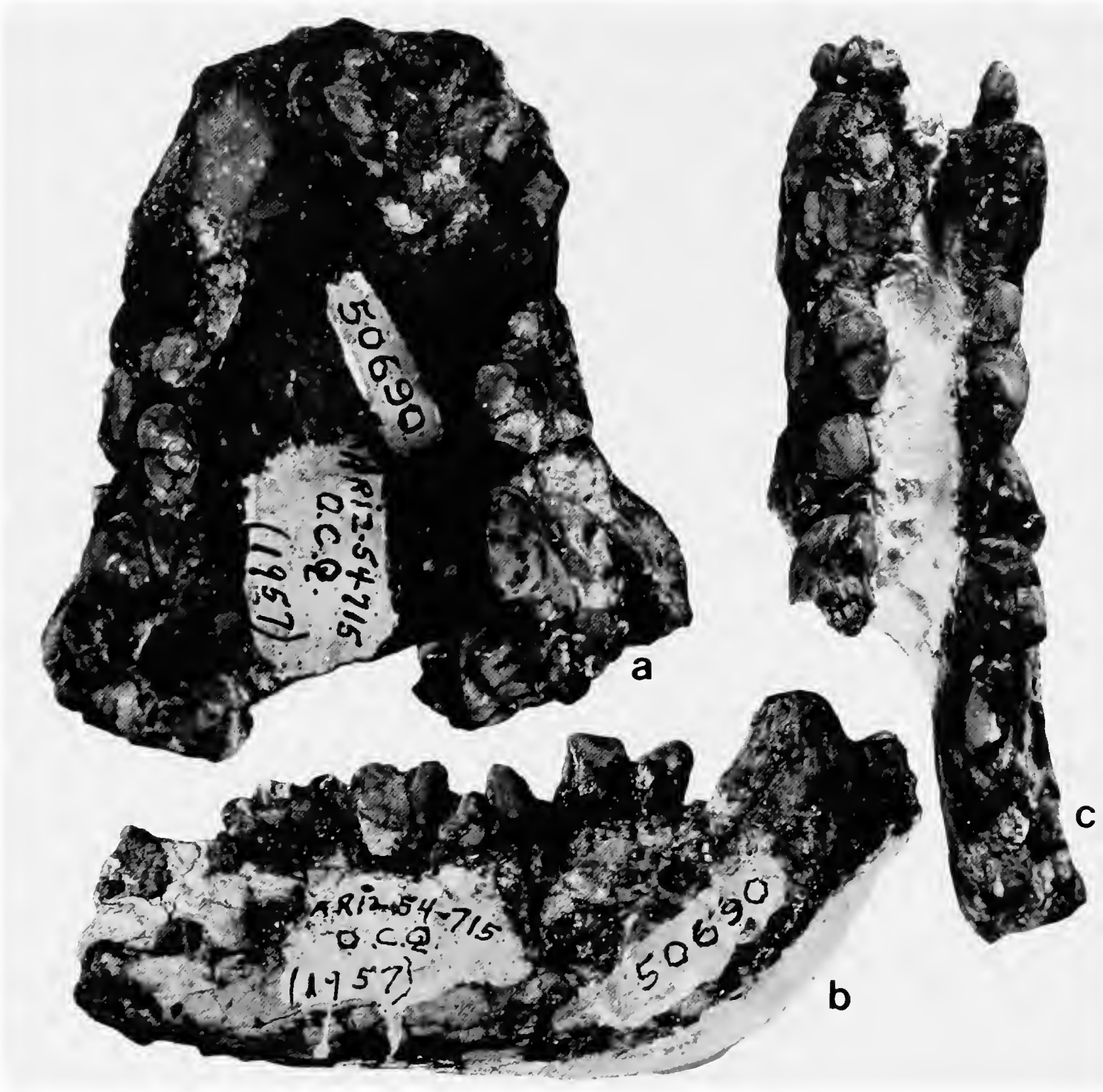

FIGURE 15—*Plesiogulo lindsayi*, new species, F:AM 50690: *a*, palate, occlusal view; *b*,*c* rami, lateral and occlusal views. (Specimens from Old Cabin Quarry; × 1.)

single-rooted M_2 is situated at the base of the ascending ramus.

The single specimen of *Plesiogulo* from Old Cabin Quarry is an associated palate and jaws, which are extensively crushed and deformed (Figure 15, Table 7). The ramus contains I_3, a tooth not present in the Wikieup sample, but the state of preservation is such that little can be said of the tooth. The size of the dentition, the depth of the ramus, the heavily crenulted enamel on C_1, and the large premolars support the referral of these specimens to *P. lindsayi*.

Two isolated canine teeth, C^1 and C_1, from a third Arizona locality, Redington Quarry, match well those from the type locality in size and degree of crenulation. An isolated left P_4 from Pinole Tuff, California, is very close in size to the mean of the P_4's from Wikieup and bears the same strong lingual bulge.

Three partial radii, two partial ulnae, and a

TABLE 7.—Measurements (cm) of *Plesiogulo lindsayi*, new species (O.R. = observed range)

Element		*No.*	*O.R.*
OLD CABIN QUARRY			
P^2	width	1	0.66
P^3	length	1	1.45
	width	1	0.87
M^1	length, lingual	1	1.51
	length, median	1	1.12
	width	1	1.97
C_1	length	1	1.81
P_2	length	1	0.87
P_3	length	1	0.73
REDINGTON QUARRY			
C^1	length	1	1.70
	width	1	1.38
C_1	length	1	1.79
	width	1	1.47
Ulna	length	1	15.81
PINOLE TUFF			
P_4	length	1	1.52
	width	1	0.95

partial ischium from Wikieup (Figure 16) and a partial ulna from Redington Quarry are referred to *P. lindsayi* (Table 7). The Redington Quarry ulna is the largest of the three; its distal end is complete, but several fragments are missing from the coronoid process and trochlear notch. One ulna from Wikieup (Figure 16 *c,d*) has an undamaged proximal end while the other has an undamaged distal end (Figure 16 *e,f*). The Redington Quarry and Wikieup ulnae bear the same long, concave olecranon process as the ulna of *P. marshalli*. The styloid process, present in two of the specimens, is heavy and rounded as in *P. marshalli*. The groove in the top of the olecranon process and the sharp posteromedial crest on the distal end are also present in the ulna of *P. lindsayi*.

The partial radii from Wikieup are very similar to those of *P. marshalli*. The two right radii are missing only the distal articular surface, but the left radius consists only of the proximal quarter. The bicipital tuberosity, the shape of the proximal articular surface, and the deep lateral groove on the distal end are all as in the radius of *P. marshalli*.

A pelvic fragment, consisting of the left ischium and the posterodorsal portion of the acetabulum, is questionably associated with an ulna (F:AM 67957) from Wikieup (Figure 16 *e,f*). The ischium is longer in *Osteoborus* than in *Plesiogulo*. The acetabulum is deeper in both *Plesiogulo* and *Gulo* than in *Osteoborus*.

The postcrania referred to *P. lindsayi* are larger than those referred to *P. marshalli*; however, this size differential is not so great as that between their respective crania and dentitions. It would appear that *P. lindsayi* had a somewhat larger body, but a much larger head than *P. marshalli*.

DISCUSSION.—Schlosser (1903:26) described as *Lutra brachygnathus* a ramus from an unknown locality in China, "allegedly from Tientsin." Zdansky (1924:38) erected the genus *Plesiogulo*, designating *L. brachygnathus* as the genotypic species, and went on to refer and describe additional material from the Paote area of Shansi Province, People's Republic of China. This material, consisting of about a dozen whole and partial crania, some with associated inferior dentitions, is housed in the Lagrelius collection at the Paleontological Institute at Uppsala. Subsequent referral of specimens to *P. brachygnathus* include a ramus from the Bhandar bone bed in the Siwaliks of Pakistan (Lewis, 1933) and a skull and three mandibles from Pavlodar, Siberia (Orlov, 1941). Teilhard de Chardin (1945) recognized three subspecies or "formes" from two new localities in China; these were *P. b. minor* from K'ingyang, Kansu, and *P. b. crassa* and *P. b. major* from Yushe, Shansi. The first two subspecies were each based on a partial skull and ramus, while the third was based on a right ramus.

Kurtén (1970) elevated Teilhard de Chardin's subspecies to specific rank and described *P. praecocidens* based on a partial ramus from Paote, Shansi. He advocated restricting the name *P. brachygnathus* to the type ramus alone and transferred to *P. crassa* the specimens from Siberia and Pakistan and all but two of the Paote specimens. Study of the much larger sample of *P. crassa* from Paote located in the America Museum of Natural History indicates that *P. minor* falls within the

FIGURE 16—*Plesiogulo lindsayi*, new species: *a,b*, F:AM 67958, right radius, anterior and posterior views; *c,d*, F:AM 105372, partial right ulna, lateral and medial views; *e,f*, F:AM 67957, right ulna, lateral and medial views. (Specimens from Wikieup; × 1.)

range of variation of *P. crassa.*

Viret (1939:12) described *P. monspessulanus*, a very large species lacking a metaconid on M_1, from Montpellier, France. Hendey (1978) referred two partial skulls, three mandibles, and assorted postcrania from Langebaanweg, South Africa. Both of the Langebaanweg M_1's were too damaged to permit an unqualified statement regarding the metaconid. Hendey (1978:333) judges that it was "either very small or absent."

Plesiogulo lindsayi most closely resembles in size *P. major* and *P. monspessulanus*. *Plesiogulo major* differs from *P. monspessulanus* in slightly larger size and a strong M_1 metaconid. Kurtén (1970:18) sugests that the presence or absence of this cusp is subject to individual variation, and Hendey (1978:343) advocates disregarding the character entirely and lumping the two taxa under *P. mon-*

spessulanus. The metaconid, however, is consistently well developed in populations of *P. lindsayi*, as well as in *P. marshalli* and *P. crassa*, and would appear to be a valid character at the specific level. The phylogenetic relationships of the Old and New World species of *Plesiogulo* are currently under study by the author and will be treated in a subsequent publication.

The WaKeeney Specimen

An isolated left M^1 (UMMP V55756) from the late Clarendonian WaKeeney Local Fauna, Trego County, Kansas, was referred to *Plesiogulo* by Wilson (1968:111). The enamel of this tooth is not crenulated and the inner lobe is not so expanded anteroposteriorly as in either *P. marshalli* or *P. lindsayi*. The paracone and metacone are more widely separated and their smoothly curved external border contrasts with the bilobate curve seen in *P. marshalli* and *P. lindsayi*. A small cusp is present slightly lingual and posterior to the metacone, which is not present in *Plesiogulo*. The WaKeeney specimen is much smaller than the smallest M^1 of *P. marshalli*; dimensions are: lingual length 1.08 cm; median length 0.81 cm, and width 1.29 cm.

The WaKeeney specimen is not *Plesiogulo*, but an undescribed species of *Mionictis* Matthew, 1924. The tooth corresponds closely to the M^1's in an undescribed partial skull (F:AM 63296) of *Mionictis* from MacAdams Quarry, Clarendon area, Texas (H. Galiano, pers. comm., 1979).

Conclusions

Remains of *Plesiogulo* from 14 North American localities are referred to two species: *P. marshalli* from Edson, Optima (Guymon), Coffee Ranch, Modesto Reservoir (Turlock Lake), McKay Reservoir, San Juan Quarry, Upper Bone Valley, White Cone, Lost Quarry, and Ordance (Westend Blowout) and *P. lindsayi*, new species, from Wikieup, Redington Quarry, Old Cabin Quarry, and Pinole Tuff. *Plesiogulo lindsayi*, new species, is distinguished from *P. marshalli* by its greater size, the placement of the P^4 protocone, the presence of a lateral cingulum on P^4, the presence of a strong lingual bulge on P^3 and P_4, and the shape of the inner lobe of M^1. The heretofore undescribed postcrania of both species are, as might be expected, reminiscent of *Gulo* in several characters.

Plesiogulo is widely distributed across the southern United States, but is nowhere abundant. Low population density may be the reason for the scarcity of fossil material. A preference for large individual territories in *Gulo* results in low population densities of that species and it is possible that a similar cause and effect was operative in populations of *Plesiogulo*.

Plesiogulo has been commonly interpreted as a forest-dweller, and thus its presence is considered indicative of woodland in the vicinity of deposition. This interpretation of *Plesiogulo* is based primarily on analogy to the extant wolverine, *Gulo*, an animal often misinterpreted as an obligate forest-dweller; *Gulo* is actually well adapted to the open tundra. *Plesiogulo* is most abundant in faunas with a large percentage of hypsodont, cursorial ungulates, suggestive of open, grassy plains. Hence, this genus need not be interpreted as a strictly woodland inhabitant.

Plesiogulo originated in Asia and migrated to North America between 7.0 and 6.5 million years ago. This taxon is known in North America only from the late Hemphillian.

Literature Cited

Baskin, J. A.
1979. Small Mammals of the Hemphill Age White Cone Local Fauna, Northeastern Arizona. *Journal of Paleontology*, 53(3):695–708, 2 figures.

Bennett, D. K.
1979. The Fossil Fauna from Lost and Found Quarries (Hemphillian: Latest Miocene), Wallace County, Kansas. *University of Kansas Museum of Natural History Occassional Paper*, 79:1–24.

Bjork, P. R.
1970. The Carnivora of the Hagerman Local Fauna (Late Pliocene) of Southwestern Idaho. *Transactions of the American Philosophical Society*, new series, 60(7):1–54.

Boellstorff, J. D.
1976. The Succession of Late Cenozoic Volcanic Ashes in the Great Plains: A Progress Report. *Kansas Geological Survey, Guidebook for the 24th Annual Meeting of the Mid-western Friends of the Pleistocene*, series 1, 1976:37–71.

Bryant, L. J.
1968. A New Genus of Mustelid from the Ellensburg Formation, Washington. *Los Angeles County Museum Contributions to Science*, 139:1–6.

Dalquest, W. W.
1969. Pliocene Carnivores of the Coffee Ranch (Type Hemphill) Local Fauna. *Bulletin of the Texas Memorial Museum*, 15:1–43.

Gill, T.
1872. Arrangement of the Families of Mammals with Analytical Tables. *Smithsonian Miscellaneous Collections*, 11(1):1–98.

Grinell, J., J. S. Dixson, and J. M. Linsdale
1937. *Furbearing Mammals of California.* Volume 1, 375 pages. Berkeley: University of California Press.

Hall, E. R., and K. R. Kelson
1959. *The Mammals of North America.* Volume 2, 536 pages. New York: Ronald Press Company.

Hendey, Q. B.
1978. Late Tertiary Mustelidae (Mammalia, Carnivora) from Langebaanweg, South Africa. *Annals of the South Africa Museum*, 76(10):329–357.

Hesse, C. J.
1936. A Pliocene Vertebrate Fauna from Optima, Oklahoma. *University of California Publication, Bulletin of the Department of Geological Sciences*, 24(3):57–70.

Hibbard, C. W.
1934. Two New Genera of Felidae from the Middle Pliocene of Kansas. *Transactions of the Kansas Academy of Science*, 37:239–255.

Izett, G. J.
1975. Late Cenozoic Sedimentation and Deformation in Northern Colorado and Adjoining Areas. *In* B. F. Curtis, editor, Cenozoic History of the Southern Rocky Mountains. *Geological Society of America Memoir*, 144:179–209.

Jackson, H. H. T.
1961. *Mammals of Wisconsin.* 504 pages. Madison: University of Wisconsin Press.

Jacobs, L. L.
1977. Rodents of the Hemphillian Age Redington Local Fauna, San Pedro Valley, Arizona. *Journal of Paleontology*, 51(3):505–519.

Krott, P.
1959. *Demon of the North.* 260 pages. New York: Knopf.
1960. Ways of the Wolverine. *Natural History*, 69:16–29.

Kurtén, B.
1970. The Neogene Wolverine *Plesiogulo* and the Origin of *Gulo* (Carnivora, Mammalia). *Acta Zoologica Fennica*, 131:1–22.

Lewis, G. E.
1933. Notice of the Discovery of *Plesiogulo brachygnathus* in the Siwalik Measures of India. *American Journal of Science*, 4:161.

MacFadden, B. J.
1977. Magnetic Polarity Stratigraphy of the Chamita Formation Stratotype (Mio-Pliocene) of North-Central New Mexico. *American Journal of Science*, 277:769–800.

MacFadden, B. J., and K. Manley
1976. Magnetic Stratigraphy, Tephrochronology, and Mammalian Biostratigraphy of the Type Chamita Formation, North-Central New Mexico. *Geological Society of America Abstracts with Programs*, 8(5):605.

MacFadden, B. J., N. M. Johnson, and N. D. Opdyke
1979. Magnetic Polarity Stratigraphy of the Mio-Pliocene Mammal-Bearing Big Sandy Formation of Western Arizona. *Earth and Planetary Science Letters*, 44:349–364.

Martin, H. T.
1928. Two New Carnivores from the Pliocene of Kansas. *Journal of Mammalogy*, 9:233–236, plates 20–21.

Matthew, W. D.
1924. Third Contribution to the Snake Creek Fauna. *Bulletin of the American Museum of Natural History*, 50(2):59–210.

Matthew, W. D., and R. A. Stirton
1930. Equidae from the Pliocene of Texas. *University of California Publication, Department of Geological Sciences*, 19(17):349–396.

Miller, G. S., Jr.
1912. *Catalogue of the Mammals of Western Europe (Europe Exclusive of Russia) in the British Museum.* 1019 pages. London: British Museum (Natural History).

Myhre, R., and S. Myrberget
1975. Diet of Wolverines (*Gulo gulo*) in Norway. *Journal of Mammalogy*, 56:752–757.

Nowak, R. M.
1973. Return of the Wolverine. *National Parks and Conservation Magazine*, 47(2):20–23.

Orlov, J. A.
1941. Tertiary Carnivora of West Siberia, III: Mustelinae. *In* J. A. Orlov, Tertiary Mammalia and the Localities of Their Remains. *Travaux de l'Institut Paleontologique, Academie des Sciences de l'Union des Republiques Sovietiques Socialistes*, 8(3):30–39.

Pocock, R. I.
1920. On the External Characters of the Ratel (*Mellivora*) and the Wolverine (*Gulo*). *Proceedings of the Zoological Society of London*, 1920:179–187.

Reed, L. C., and O. M. Longnecker, Jr.
1932. The Geology of Hemphill County, Texas. *University of Texas Bulletin*, 3231:1–98.

Savage, D. E.
1941. Two New Middle Pliocene Carnivores from Oklahoma with Notes on the Optima Fauna. *American Midland Naturalist*, 25(3):692–710.

Scarborough, R. B., P. E. Damon, and M. Shafiqullah
1974. K-Ar Age for a Basalt from the Volcanic Member (Unit 5) of the Bidahochi Formation. *Geological Society of America Abstracts with Programs*, 6(5):472.

Schlosser, M.
1903. Die fossilen Saugetheire Chinas nebst einer Odontographie der recenten Antilopen. *Abhandlungen der Bayerischen Akademie der Wissenschaften*, 22(1):1–22.

Schultz, G. E.
1977. Guidebook for the Field Conference on Late Cenozoic Biostratigraphy of the Texas Panhandle and Adjacent Oklahoma. *Kilgore Research Center Special Publication*, 1:1–160.

Sellards, E. H., W. S. Adkins, and F. B. Plummer
1932. The Geology of Texas, Volume 1: Stratigraphy. *University of Texas Bulletin*, 3232:1–1770.

Seton, E. T.
1929. *Lives of Game Animals.* Volume 2, part 2, 746 pages. Garden City: Doubleday, Doran, and Company, Inc.

Shotwell, J. A.
1955. An Approach to the Paleoecology of Mammals. *Ecology*, 36(2):327–337.

1956. Hemphillian Mammalian Assemblage from Northeastern Oregon. *Geological Society of America Bulletin*, 67:717–738.

1958. Inter-community Relationships in Hemphillian (Mid-Pliocene) Mammals. *Ecology*, 39(2):271–282.

Slaughter, B. H., R. H. Pine, and N. E. Pine
1974. Eruption of Cheek Teeth in Insectivora and Carnivora. *Journal of Mammalogy*, 55(1):115–125.

Teilhard de Chardin, P.
1945. Les Mustélidés de Chine. *Institut de Géobiologie, Pékin*, 12:1–56.

Viret, J.
1939. Monographie Paléontologique de la Faune de Vertébrés des Sable de Montpellier, III: Carnivora, Fissipedia. *Travaux du Laboratoire de Géologie de la Faculte Sciences de Lyon*, 37:5–26.

Walker, E. P.
1964. *Mammals of the World.* 2 volumes, 1500 pages. Baltimore: Johns Hopkins University Press.

Webb, S. D.
1969. The Burge and Minnechaduza Clarendonian Mammalian Faunas of North-Central Nebraska. *University of California Publications in Geological Sciences*, 78:1–191.

Wilson, R. L.
1968. Systematics and Faunal Analysis of a Lower Pliocene Vertebrate Assemblage from Trego County, Kansas. *Contributions from the Museum of Paleontology, University of Michigan*, 22(7):75–126.

Wood, H. E., R. W. Chaney, J. Clark, E. H. Colbert, G. L. Jepsen, J. B. Reeside, Jr., and C. Stock
1941. Nomenclature and Correlation of the North American Continental Tertiary. *Geological Society of America Bulletin*, 52:1–48.

Zdansky, O.
1924. Jungtertiäre Carnivoren Chinas. *Paleontologica Sinica*, series C, 2(1):1–155.

REQUIREMENTS FOR SMITHSONIAN SERIES PUBLICATION

Manuscripts intended for series publication receive substantive review within their originating Smithsonian museums or offices and are submitted to the Smithsonian Institution Press with approval of the appropriate museum authority on Form SI–36. Requests for special treatment—use of color, foldouts, casebound covers, etc.—require, on the same form, the added approval of designated committees or museum directors.

Review of manuscripts and art by the Press for requirements of series format and style, completeness and clarity of copy, and arrangement of all material, as outlined below, will govern, within the judgment of the Press, acceptance or rejection of the manuscripts and art.

Copy must be typewritten, double-spaced, on one side of standard white bond paper, with 1¼" margins, submitted as ribbon copy (not carbon or xerox), in loose sheets (not stapled or bound), and accompanied by original art. Minimum acceptable length is 30 pages.

Front matter (preceding the text) should include: **title page** with only title and author and no other information, **abstract page** with author/title/series/etc., following the established format, **table of contents** with indents reflecting the heads and structure of the paper.

First page of text should carry the title and author at the top of the page and an unnumbered footnote at the bottom consisting of author's name and professional mailing address.

Center heads of whatever level should be typed with initial caps of major words, with extra space above and below the head, but with no other preparation (such as all caps or underline). Run-in paragraph heads should use period/dashes or colons as necessary.

Tabulations within text (lists of data, often in parallel columns) can be typed on the text page where they occur, but they should not contain rules or formal, numbered table heads.

Formal tables (numbered, with table heads, boxheads, stubs, rules) should be submitted as camera copy, but the author must contact the series section of the Press for editorial attention and preparation assistance before final typing of this matter.

Taxonomic keys in natural history papers should use the alined-couplet form in the zoology and paleobiology series and the multi-level indent form in the botany series. If cross-referencing is required between key and text, do not include page references within the key, but number the keyed-out taxa with their corresponding heads in the text.

Synonymy in the zoology and paleobiology series must use the short form (taxon, author, year:page), with a full reference at the end of the paper under "Literature Cited." For the botany series, the long form (taxon, author, abbreviated journal or book title, volume, page, year, with no reference in the "Literature Cited") is optional.

Footnotes, when few in number, whether annotative or bibliographic, should be typed at the bottom of the text page on which the reference occurs. Extensive notes must appear at the end of the text in a notes section. If bibliographic footnotes are required, use the short form (author/brief title/page) with the full reference in the bibliography.

Text-reference system (author/year/page within the text, with the full reference in a "Literature Cited" at the end of the text) must be used in place of bibliographic footnotes in all scientific series and is strongly recommended in the history and technology series: "(Jones, 1910:122)" or ". . . Jones (1910:122)."

Bibliography, depending upon use, is termed "References," "Selected References," or "Literature Cited." Spell out book, journal, and article titles, using initial caps in all major words. For capitalization of titles in foreign languages, follow the national practice of each language. Underline (for italics) book and journal titles. Use the colon-parentheses system for volume/number/page citations: "10(2):5–9." For alinement and arrangement of elements, follow the format of the series for which the manuscript is intended.

Legends for illustrations must not be attached to the art nor included within the text but must be submitted at the end of the manuscript—with as many legends typed, double-spaced, to a page as convenient.

Illustrations must not be included within the manuscript but must be submitted separately as original art (not copies). All illustrations (photographs, line drawings, maps, etc.) can be intermixed throughout the printed text. They should be termed **Figures** and should be numbered consecutively. If several "figures" are treated as components of a single larger figure, they should be designated by lowercase italic letters (underlined in copy) on the illustration, in the legend, and in text references: "Figure 9*b*." If illustrations are intended to be printed separately on coated stock following the text, they should be termed **Plates** and any components should be lettered as in figures: "Plate 9*b*." Keys to any symbols within an illustration should appear on the art and not in the legend.

A few points of style: (1) Do not use periods after such abbreviations as "mm, ft, yds, USNM, NNE, AM, BC." (2) Use hyphens in spelled-out fractions: "two-thirds." (3) Spell out numbers "one" through "nine" in expository text, but use numerals in all other cases if possible. (4) Use the metric system of measurement, where possible, instead of the English system. (5) Use the decimal system, where possible, in place of fractions. (6) Use day/month/year sequence for dates: "9 April 1976." (7) For months in tabular listings or data sections, use three-letter abbreviations with no periods: "Jan, Mar, Jun," etc.

Arrange and paginate sequentially EVERY sheet of manuscript—including ALL front matter and ALL legends, etc., at the back of the text—in the following order: (1) title page, (2) abstract, (3) table of contents, (4) foreword and/or preface, (5) text, (6) appendixes, (7) notes, (8) glossary, (9) bibliography, (10) index, (11) legends.